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All papers in the Bulletin which have been thus shortened, will be marked at the end by the symbol MF, followed by a figure, indicating the number of double-spaced typewritten pages of the unabbreviated manuscript.

MATHEMATICAL THEORY OF MOTIVATION INTERACTIONS OF TWO INDIVIDUALS: II

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The behavior of two individuals, consisting of effort which results in output, is considered to be determined by a satisfaction function which depends on remuneration (receiving part of the output) and on the effort expended. The total output of the two individuals is not additive, that is, together they produce in general more than separately. Each individual behaves in a way which he considers will maximize his satisfaction function. Conditions are deduced for a certain relative equilibrium and for the stability of this equilibrium, i.e., conditions under which it will not "pay" the individual to decrease his efforts. In the absence of such conditions "exploitation" occurs which may or may not lead to total parasitism. Some forms of the inverse problem are considered, where the form of behavior is given and forms of the satisfaction function are deduced which lead to it.

In a previous paper (Rapoport, 1947), hereafter referred to as I, we assumed that the total output of two individuals equals the sum of their individual outputs. As in I, we define x and y as the respective efforts (and outputs) of two individuals X and Y, whose satisfaction functions are given by

$$S_i = R_i(x, y) + E_i(x, y), \quad i = 1, 2, \tag{1}$$

where R_i, essentially positive, represents the contribution to satisfaction by remuneration received, and E_i, essentially negative, the detraction from satisfaction by effort expended. We shall call an optimal curve for X, the set of points (x, y) at which $\partial S_1/\partial x = 0$, and an optimal curve for Y, the set of points (x, y) at which $\partial S_2/\partial y = 0$. Each individual then behaves in such a way (increases or decreases his output) as to reach a point on his optimal curve.

We have shown in I that when total output is additive and is equally shared, the optimal curves for both individuals are represented by the same straight line

$$x + y = \frac{1}{\beta} - 2. \tag{2}$$

Each point on that common optimal curve was shown to be unstable in the sense that a small decrease of effort on the part of one in-

dividual resulted in an increased effort on the part of the other ulti-
mately leading to "complete parasitism" (see Figure 1). Furthermore,
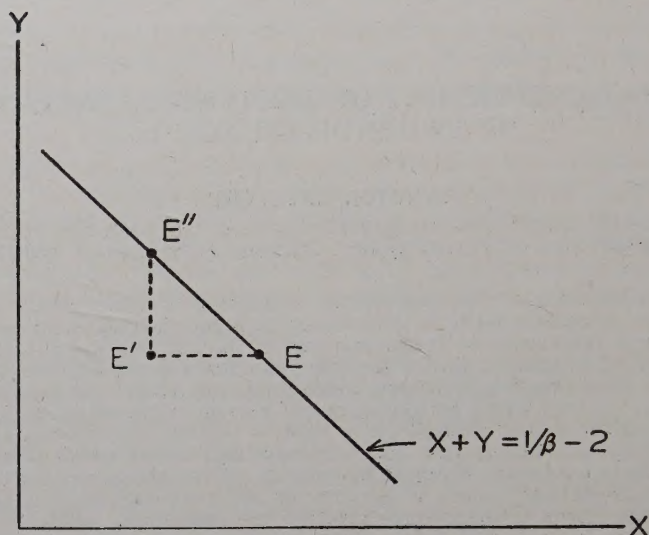
<div align="center">FIGURE 1</div>

Every point of the line $x + y = 1/\beta - 2$ is an unstable "point of agreement."
If X decreases his output from E to E', Y will increase his output to E''. The
point E'' is a point of greater satisfaction for X, and he may repeat the process
until his output is zero (complete parasitism).

it was impossible under those conditions to find a point on the optimal
curve which could be distinguished in any way as a "point of agree-
ment" for the two individuals.

By a "point of agreement" we mean a point $(\bar{x}, \bar{y})$ which is a
projection on the xy-plane of a point of the intersection curve of
$S_1(x, y)$ and $S_2(x, y)$ which is characterized by certain maximum
properties. If we demand that the "point of agreement" be a "total
maximum" of both surfaces, to be defined below, the conditions on the
partial derivatives of S_i with respect to x and y are very stringent
[see equations (54)]. If, on the other hand, we weaken these condi-
tions and demand only that

$$\frac{\partial S_1}{\partial x} = 0; \quad \frac{\partial S_2}{\partial y} = 0; \quad \frac{\partial^2 S_1}{\partial x_2{}^2} < 0; \quad \frac{\partial^2 S_2}{\partial y_2{}^2} < 0, \tag{3}$$

then *every* point of the optimal curve in Figure 1 is a "point of agree-
ment."

We seek a situation in which the "point of agreement" satisfying
equations (3) is unique at least in a suitable region. We shall then in-
vestigate the conditions of stability at such points.

In I we have considered six cases of motivation interactions of two individuals. We have numbered the cases in this paper consecutively with those of I.

Case VII. *The output is increased in joint production by a quantity proportional to the product of the outputs. Equal sharing. Determination of output by simultaneous maximizing of S_1 and S_2.*

The failure of the preceding system to give satisfactions greater than those achieved under individual production except in situations involving the exploitation of one individual by another, is traced, of course, to the decreased initiative on the part of the individuals to produce when maximum satisfactions are computed by partial differentiation (since each individual's increased output is now split between himself and his neighbor). In partial differentiation, no account is taken of possible effects on the output of the second individual by the behavior of the first. We have seen how the introduction of contracts does account for such effects. We shall here consider incentives other than contracts. Let the efficiency of production increase with joint production (say by division of labor) by an amount proportional to the product of the individual efforts, so that for no effort on the part of one individual, the output reduces to the individual output of the other. Therefore, let the total output be given by

$$T = x + y + \alpha xy .\tag{4}$$

We shall refer to α as the cooperation coefficient. Then

$$S_1 = \log\left[1 + \frac{x + y + \alpha xy}{2} \right] - \beta x ,$$

$$\tag{5}$$

$$S_2 = \log\left[1 + \frac{x + y + \alpha xy}{2} \right] - \beta y .$$

The system

$$\frac{\partial S_1}{\partial x} = 0 ; \quad \frac{\partial S_2}{\partial y} = 0 ;$$

$$\tag{6}$$

$$\frac{1 + \alpha x}{2 + x + y + \alpha xy} - \beta = 0 ; \quad \frac{1 + \alpha y}{2 + x + y + \alpha xy} - \beta = 0$$

now yields a unique pair of solutions for x and y, namely

$$\bar{x} = \bar{y} = \frac{\alpha - 2\beta \pm Q}{2\alpha\beta} ,\tag{7}$$

where

$$Q \equiv \sqrt{\alpha^2 - 8\alpha\beta^2 + 4\beta^2} .$$

We choose the plus sign for the radical (the other solution is not a maximum) and substituting into equation (5) get

$$S_1{}^* = S_2{}^* = \log(\alpha + Q) - \log 4\,\beta^2 - \frac{\alpha - 2\beta + Q}{2\,\alpha}. \qquad (8)$$

First let us note the limit of $S_i{}^*$ as α approaches zero. That of the first two terms is $\log \dfrac{1}{2\,\beta}$. Evaluating the last term by L'Hôpital's Rule, we get

$$\operatorname*{Lim}_{\alpha \to 0} \frac{\alpha - 2\,\beta + Q}{2\,\alpha} = \frac{1}{2} - \beta \quad (\text{NB: } \lim_{\alpha \to 0} Q = 2\,\beta).$$

Hence $\operatorname*{Lim}_{\alpha \to 0} S_i{}^* = \dfrac{1}{2\,\beta} - \dfrac{1}{2} + \beta$, which is exactly the value of $S_1{}^* = S_2{}^*$ in Case III of I for $k = \frac{1}{2}$. But in Case III there was no way to come to this "agreement," by simultaneous solution of the system

$$\frac{\partial S_1}{\partial x} = 0; \quad \frac{\partial S_2}{\partial y} = 0.$$

With the added motivation of the cooperation coefficient, no matter how small, such a possibility for agreement by *simultaneous* partial differentiation exists.

Let us now see how $S_i{}^*$ behaves with respect to α. We have

$$\frac{\partial S_i{}^*}{\partial \alpha} = \frac{1 + \dfrac{\alpha - 4\,\beta^2}{Q}}{\alpha + Q} - \frac{2\,\alpha\left[1 + \dfrac{\alpha - 4\,\beta^2}{Q}\right] - 2(\alpha - 2\,\beta + Q)}{4\,\alpha^2}.$$

The limit of the first term as $\alpha \to 0$ is $\dfrac{1 - 2\,\beta}{2\,\beta}$. The limit of the second term is indeterminate but can be evaluated by L'Hôpital's Rule. After two differentiations we find it to be $\dfrac{-4\,\beta^2 + 1}{8\,\beta}$. Hence

$$\operatorname*{Lim}_{\alpha \to 0} \frac{\partial S_i{}^*}{\partial \alpha} = \frac{4\,\beta^2 - 8\,\beta + 3}{8\,\beta} > 0 \quad \text{for } \beta < \tfrac{1}{2}.$$

Therefore, production is possible for $\beta < \frac{1}{2}$ for all values of $\alpha > 0$. It can also be shown that if $\bar{x}$ is the maximizing value of the argument, then $\dfrac{\partial \bar{x}}{\partial \alpha} > 0$ for $\beta < \frac{1}{2}$, that is, the cooperation coefficient is an

incentive for greater optimum output.

The solutions of $\dfrac{\partial S_1}{\partial x} = 0$ and $\dfrac{\partial S_2}{\partial y} = 0$ lie along two curves, namely,

$$y_1 = \frac{1 - 2\beta - \beta x_1}{\alpha \beta x_1 + \beta - \alpha}; \quad y_2 = \frac{1 - 2\beta - \beta x_2 - \alpha x_2}{\alpha \beta x_2 + \beta}.$$

An intersection of these two curves is the point $(\bar{x}, \bar{y})$, where

$$\bar{x} = \frac{\alpha - 2\beta + Q}{2\alpha\beta} = \bar{y}$$

and $Q = \sqrt{\alpha^2 - 8\alpha\beta^2 + 4\beta^2}$. For the intersection to be real, we must have

$$\alpha^2 - 8\alpha\beta^2 + 4\beta^2 > 0. \tag{9}$$

That this is always the case for $\beta < \frac{1}{2}$ is seen from the following considerations (NB: $\beta < \frac{1}{2}$ holds throughout the discussion, since it is a necessary condition for production to start). For $\beta = \frac{1}{2}$, the left side of relation (9) reduces to $\alpha^2 - 2\alpha + 1$, which is positive for all values of α. It remains to examine two cases: 1) $\beta < \frac{1}{2}$, $\alpha < \frac{1}{2}$ and 2) $\beta < \frac{1}{2}$, $\alpha > \frac{1}{2}$. Let $\alpha < \frac{1}{2}$. Then $\alpha^2 - 8\alpha\beta^2 + 4\beta^2 = \alpha^2 - 4\beta^2(2\alpha - 1)$. But $2\alpha - 1$ is negative if $\alpha < \frac{1}{2}$, hence $Q^2 > 0$. Now let $\alpha > \frac{1}{2}$. Write $Q^2 = \alpha^2 + 4\beta^2(1 - 2\alpha)$ and note that the second term is negative. But we have shown that $Q^2 > 0$ for $\beta = \frac{1}{2}$. Reducing β reduces the only negative term, hence $Q^2 > 0$ if $\beta < \frac{1}{2}$. In all cases considered the two optimal curves will intersect in a real point. Let us consider the "stability" of the system at that point.

By stability of a system we understand a situation where it does not pay for an individual to lower his output. In this sense the system based on equal sharing without contract considered in Case III of I was not stable. For suppose X to be an "active" individual, i.e., capable of effecting changes in his behavior not merely on the basis of *immediate* increase of satisfaction, but with a view toward future events. Starting from any position of equilibrium in Case III, suppose X lowers his output. Since the position of equilibrium was a maximizing position for S_1, this change has for its immediate result a decrease in S_1, X's satisfaction. But Y, acting entirely on the principle of immediate maximizing of S_2, increases his output so as to get back to the optimal line (See Figure 1). Thus a new point of equilibrium E'' is reached, at which point the satisfaction of X is greater than at E, while that of Y is less. This process can theoretically continue until X has become parasitic on Y, barring such phe-

nomena as the increase of "activeness" with decrease of satisfaction, which would cause Y ultimately to resist such a process. In a stable system, on the other hand, a decrease in output on the part of one individual would have for its end result a decrease in his satisfaction function. Nothing has been said here about the effects of *increasing* output on the part of an active individual. Theoretically, situations can exist where such an increase causes an increase in the output of the other, and so on indefinitely. Such cases are of no interest because of the obvious physical limitations to increase of effort, limitations not expressed in the equations and therefore extraneous to the problem.

In the present case, the situation is considerably different from that in Case III. We are dealing with two separate, nonlinear optimal curves, instead of two coincident linear ones (see Figure 2).

$$Y = \frac{1-2\beta-\beta X}{\alpha\beta X + \beta - \alpha}$$

$$Y = \frac{1-2\beta+(\alpha-\beta)X}{\alpha\beta X + \beta}$$
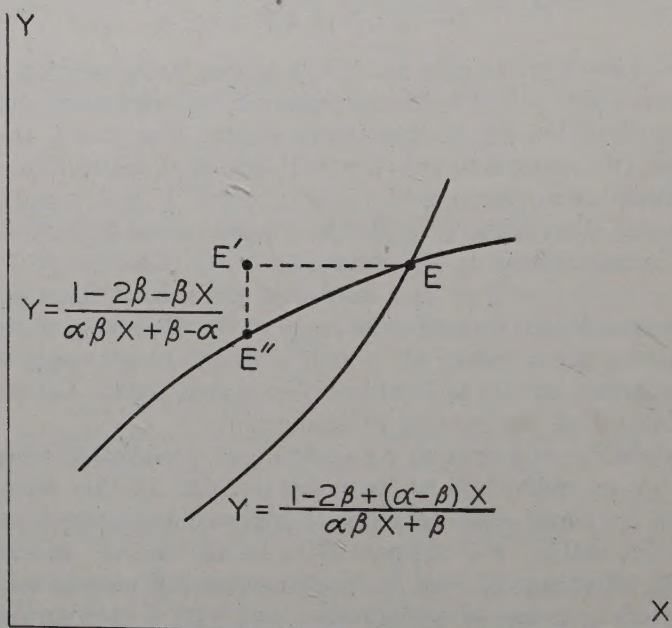
FIGURE 2

Optimal curves in the case of non-additive total output. If X decreases his output from E to E', Y will bring his own output to the point E'' on his own optimal curve. For $\alpha > \frac{1}{2}$, this results in a decrease of satisfaction for X.

If X now gets off the point of equilibrium by decreasing his effort, Y will tend to bring the production back to his own optimal curve, distinct from that of X. To see how that will affect X's satisfaction function ultimately, we must take the directional derivative of S_1 in the direction of the S_2 optimal curve. Let us compute the

slopes of the optimal curves at $\bar{x}$, $\bar{y}$, their point of intersection. We have

$$y'_1 = \frac{\beta^2 (2\,\alpha - 1)}{(\alpha\,\beta\,x_1 + \beta - \alpha)^2}; \tag{10}$$

$$y'_2 = \frac{\beta^2 (2\,\alpha - 1)}{(\alpha\,\beta\,x_1 + \beta)^2}; \tag{11}$$

$$y'_1 \Big|_{y_1 = \bar{y}} = \frac{4\,\beta^2 (2\,\alpha - 1)}{(Q - \alpha)^2}; \tag{12}$$

$$y'_2 \Big|_{y_2 = \bar{y}} = \frac{4\,\beta^2 (2\,\alpha - 1)}{(Q + \alpha)^2}. \tag{13}$$

If θ_1 and θ_2 are the respective inclinations of the tangents to the optimal curves at $(\bar{x}, \bar{y})$, we have

$$\tan \theta_1 = y'_1 \Big|_{y_1 = \bar{y}},$$

$$\tan \theta_2 = y'_2 \Big|_{y_2 = \bar{y}}.$$

Also $\sin \theta_1 \geqq 0$ and $\sin \theta_2 \geqq 0$ since θ_1 and θ_2 are taken between 0 and π.

We seek the directional derivative of S_1 in the direction θ_2:

$$\frac{\partial S_1}{\partial s} \Big|_{\theta_2} = \frac{\partial S_1}{\partial x} \cos \theta_2 + \frac{\partial S_1}{\partial y} \sin \theta_2.$$

But $\dfrac{\partial S_1}{\partial x} = 0$ at $(\bar{x}, \bar{y})$ and $\dfrac{\partial S_1}{\partial y} = \dfrac{1 + \alpha\,x}{2 + x + y + \alpha\,x\,y}$, hence both derivatives are positive for all non-negative values of x and y. Therefore

$$\frac{\partial S_1}{\partial s} \geqq 0. \tag{14}$$

Observe, however, that for $\alpha < \frac{1}{2}$, $\tan \theta_2 < 0$. Therefore, for $\alpha < \frac{1}{2}$, the θ_2 direction corresponds to *decreasing* x. First let $\alpha < \frac{1}{2}$. Then if x has decreased and the production has been restored to the optimal curve of Y, the point (x, y) has moved in the θ_2 direction. Since by equation (14) the directional derivative is always positive, S_2 has been increased by the decrease in x. Thus for $\alpha < \frac{1}{2}$, the equilibrium

is unstable at $(\bar{x}, \bar{y})$. If, however, $\alpha > \frac{1}{2}$, $\tan \theta > 0$, decreasing of x and restoration of (x, y) to the optimal curve of Y moves the point in the direction opposite to θ_2. Since the directional derivative is still positive, this results in a *decrease* of satisfaction for X. He will therefore tend not to decrease his effort. On the contrary, he may tend to increase it indefinitely, unless other factors (such as decline in efficiency for very high values of x and y, or increase of reluctance or any other stabilization of the system) interfere. We therefore state

Theorem 7. *If the satisfactions are given by equations* (5), *an optimum output can be agreed upon by simultaneous maximizing of the satisfaction functions partially with respect to the respective variables. The system is stable at the optimum output if and only if* $\alpha \geqq \frac{1}{2}$.

Case VIII. *Determining the output from the point of view of* X. Now let X be active, i.e., X considers the situation in advance and has some knowledge about the behavior of Y. Then X considers that Y will try to maximize his satisfaction function, i.e., try to bring it onto his own optimal curve. Therefore X takes the value of y given by $\dfrac{\partial S_2}{\partial y} = 0$, that is,

$$y = \frac{1 - 2\beta - \beta x + \alpha x}{\alpha \beta x + \beta}. \tag{15}$$

Substituting this value into S_1 and differentiating now totally with respect to x gives for optimum output

$$\bar{x} = \frac{\alpha - \beta}{\alpha \beta}. \tag{16}$$

The individual X lets Y determine his optimum output according to equation (15). Thus

$$\bar{y} = \frac{\alpha^2 - \alpha \beta - 2 \alpha \beta^2 + \beta^2}{\alpha^2 \beta}. \tag{17}$$

Substituting the values of x and y given by expressions (16) and (17) into $S_1(x, y)$, we get

$$\overline{S}_1 = \log \left(\frac{\alpha}{2 \beta^2} \right) - \frac{\alpha - \beta}{\alpha},$$

$$\overline{S}_2 = \log \left(\frac{\alpha}{2 \beta^2} \right) - \frac{\alpha^2 - \alpha \beta - 2 \alpha \beta^2 + \beta^2}{\alpha^2}. \tag{18}$$

Elementary computations show that, in effect, a stable equilibrium with

respect to X's behavior has been reached. This point of stable equilibrium could have been computed also from the preceding case by setting the proper directional derivative equal to zero. We can now examine in detail the state of affairs determined by the "active individual" simply through his superior knowledge of the situation. In particular, we can compare the resulting satisfactions with those characteristic of the simultaneous solution equilibrium. We shall see what changes have occurred in Y's (the passive individual's) satisfaction function. Finally, we can compute the value of α for which it becomes profitable for one or both individuals to enter joint production under sharing.

We note first of all from equation (16) that if $\alpha \leqq \beta$, $\bar{x} \leqq 0$. Since only non-negative values are considered, we see that the condition leads to parasitism by active X upon passive Y if $\alpha \leqq \beta$. In that case,

$$S_1 = \log\left(\frac{1}{2\beta}\right),$$

$$S_2 = \log\left(\frac{1}{2\beta}\right) - 1 + 2\beta,$$

exactly as in the corresponding degenerate case (complete parasitism) in Case III.

If $\alpha > \beta$, a point of equilibrium short of complete parasitism is reached.

Theorem 8.   *Parasitism will occur in Case VIII if and only if* $\alpha \leqq \beta$.

Therefore, let $\alpha > \beta$. We have

$$\frac{\partial S_1}{\partial \alpha} = \frac{1}{\alpha} - \frac{\beta}{\alpha^2} = \frac{1}{\alpha}\left(1 - \frac{\beta}{\alpha}\right) > 0$$

$$\frac{\partial \bar{x}}{\partial \alpha} = \frac{1}{\alpha^2} > 0,$$

and we see that for greater α, X will choose a point of greater effort for himself, but his resulting satisfaction will also be greater.

Let us now compare $\bar{S}_1$ as given by expression (18) with that given by equation (8) and see under what conditions the former will exceed the latter; in other words, we wish to see whether the foresight exhibited by X will always pay under these conditions.

The difference in the two satisfactions is

$$\log \frac{\alpha}{2\,\beta^2} - \frac{\alpha - \beta}{\alpha} - \log(\alpha + Q) + \log 4\,\beta^2 + \frac{\alpha - 2\,\beta + Q}{2\,\alpha}$$

$$= \log \frac{2\,\alpha}{\alpha + Q} - \frac{1}{2} + \frac{Q}{2\,\alpha} \equiv D_1(\alpha).$$

Note that $D_1(\tfrac{1}{2}) = 0$ since $Q(\tfrac{1}{2}) = \tfrac{1}{2} = \alpha$.

Consider now that

$$D'_1(\alpha) = \frac{2\,\beta^2\,(\alpha - Q)\,(1 - \alpha)}{\alpha^2\,Q\,(\alpha + Q)}.$$

Examining $Q(\alpha) = \sqrt{\alpha^2 - 4\,\beta^2\,(2\,\alpha - 1)}$, we see that $\alpha < Q$ if, and only if, $\alpha < \tfrac{1}{2}$. Hence
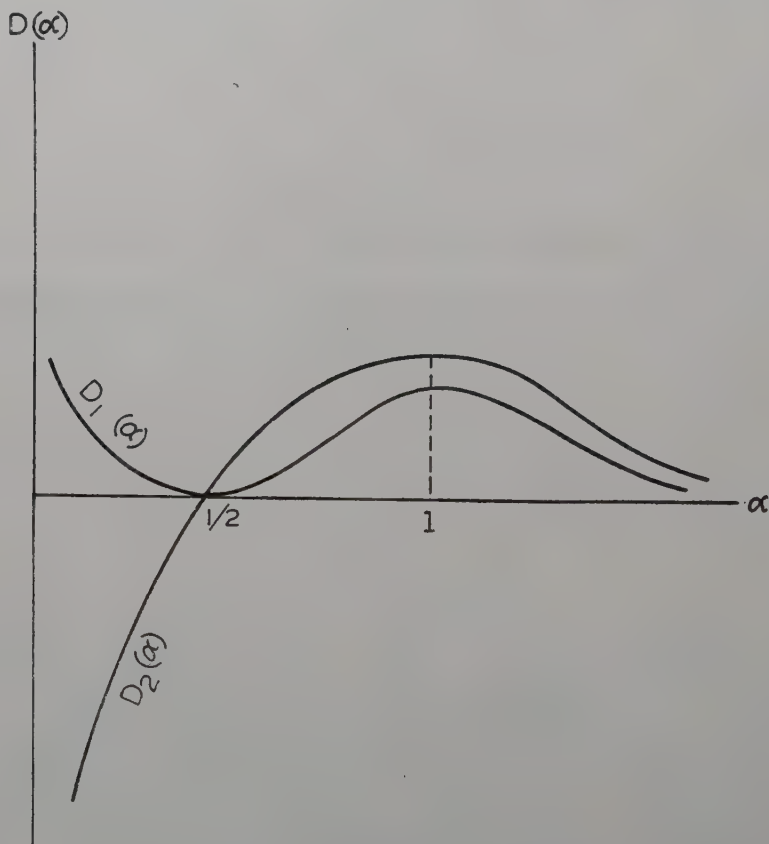

FIGURE 3

Comparison of advantages to X and Y, when X assumes "leadership" under conditions of Case VIII.

$$D_1'(\alpha) < 0 \text{ for } \alpha < \tfrac{1}{2},$$
$$D_1'(\alpha) = 0 \text{ for } \alpha = \tfrac{1}{2},$$
$$D_1'(\alpha) > 0 \text{ for } \tfrac{1}{2} < \alpha < 1,$$
$$D_1'(\alpha) < 0 \text{ for } \alpha > 1,$$
$$\mathrm{Lim}_{\alpha \to \infty} D'(\alpha) = 0.$$

This examination of $D_1'(\alpha)$, plus the fact that $D(\tfrac{1}{2}) = 0$, enables us at once to draw a graph of $D_1(\alpha)$ (see Figure 3). We see that the satisfaction of X arrived at by his computation (Case VIII) is greater than that arrived at by simultaneous partial differentiation (Case VII). However, referring to Theorem 7, we see that for $\alpha < 1/2$, X tends to decrease his efforts to reach the new equilibrium, while for $\alpha > 1/2$, he tends to increase them. In the first case, he will arrive at greater satisfaction by simply exploiting Y; in the second case, he himself will also increase his efforts.

It remains to consider how Y's satisfaction will be affected by the manipulations of X. Again as above we take the difference in Y's satisfactions as given by equations (8) and (18). The difference is

$$D_2(\alpha) = \log(2\,\alpha) - \log(\alpha + Q) + \frac{Q}{2\,\alpha} - \frac{1}{2} + \frac{2\,\beta^2}{\alpha} - \frac{\beta^2}{\alpha^2}$$

$$= D_1(\alpha) + \frac{\beta^2(2\,\alpha - 1)}{\alpha^2}. \tag{19}$$

The superimposed graphs of $D_1(\alpha)$ and $D_2(\alpha)$ are shown in Figure 3. Under the conditions of Case VIII, it is always advantageous for X to assume "leadership". The degree of advantage is given by the value of $D_1(\alpha)$. The value of $D_2(\alpha)$ represents the advantage to Y in accepting the leadership of X. This becomes positive for $\alpha > \tfrac{1}{2}$. When $\alpha > \tfrac{1}{2}$, it is even more advantageous for Y to accept X's leadership than it is for X to assume it.

It remains to consider under what conditions X will join the system in Case VII and in Case VIII. When X works alone, his maximal satisfaction is given by equation (5) of Case I of I.

$$S_{\max} = -\log \beta + \beta - 1.$$

This subtracted from X's satisfaction gives in Case VIII [cf. equation (8)]

$$D_1(\alpha, \beta) = \log(\alpha + Q) - 4\,\beta^2 - \frac{\alpha - 2\,\beta + Q}{2\,\alpha} - \beta + \log \beta - 1. \tag{20}$$

Thus $D_1(\alpha, \beta) > 0$ if

$$\log\left(\frac{\alpha + Q}{4\beta}\right) > \frac{2\alpha\beta + Q - 2\beta - \alpha}{2\alpha}. \tag{21}$$

For the critical value $\alpha = 1/2$, the condition on β is especially simple, namely,

$$\log 4\beta < \beta. \tag{22}$$

Since the satisfactions in Case VII are equal, similar conditions hold for Y. We summarize these results in

Theorem 10. *Sufficient motivation for either individual to co-operate and share under the conditions of Case VII is given by relation (21). For the minimum value of α which gives a stable equilibrium ($\alpha = 1/2$), the upper limit on β is given by relation (22).*

For Case VIII, the conditions are less stringent for X, since, as we have seen, X always increases his satisfaction over that of Case VII. We have for X

$$D_1(\alpha, \beta) = \log\frac{\alpha}{2\beta} + \frac{\beta}{\alpha} - \beta. \tag{23}$$

This is positive if

$$\log\left(\frac{\alpha}{2\beta}\right) > \frac{\alpha\beta - \beta}{\alpha}. \tag{24}$$

We note that $\dfrac{\partial D}{\partial \beta} = -\dfrac{1}{\beta} + \dfrac{1}{\alpha} - 1 < 0$ for $\alpha > \beta$. Hence if we let β be $1/2$, its maximum value, we can deduce a simple *sufficient* condition on α for the non-parasitic case, namely

$$\log \alpha + \frac{1}{2\alpha} > 1/2. \tag{25}$$

We see that if β is sufficiently small, relation (24) will always hold if α is fixed and finite, but not necessarily if α also approaches zero. In the parasitic case $S_1 = \log\left(\dfrac{\alpha}{2\beta^2}\right)$,

$$D_1(\alpha, \beta) = \log\left(\frac{\alpha}{\beta}\right) + 1 - \log 2 - \beta. \tag{26}$$

If $\alpha = \beta$, the arrangement will pay if $\beta < 1 - \log 2$, which is the condition on β in the parasitic situation in Case III of I.

We should expect the condition for Y to join X to be more stringent in Case VIII since Y is to play a passive role. However, this is not always the case. We have for Y,

$$D_2(\alpha, \beta) = \log\left(\frac{\alpha}{2\,\beta^2}\right) - \frac{\alpha^2 - \alpha\beta - 2\,\alpha\beta^2 + \beta^2}{\alpha^2} + \log\beta - \beta + 1. \quad (27)$$

This is positive if

$$\log\left(\frac{\alpha}{2\,\beta'}\right) > \frac{\alpha\beta - \beta}{\alpha} + \frac{\beta^2}{\alpha^2}(1 - 2\,\alpha), \quad (28)$$

and we have the curious result that for $\alpha > 1/2$ it is even more advantageous for Y to join X under X's leadership than it is for X to enter the arrangement (see Figure 3).

Case IX. *The individuals increase their output by imitation.* Let us now consider a situation similar to that in Case III of I, except that in addition to the effort which each individual expends to satisfy his own satisfaction function, he also expends additional effort in proportion to the effort of the other. In other words, we are dealing with imitative behavior. The equations connecting the variables are now

$$x = \frac{1}{\beta} - 2 - y + ky,$$

$$(29)$$

$$y = \frac{1}{\beta} - 2 - x + kx.$$

The optimal curves are now two distinct straight lines intersecting at

$$\bar{x} = \bar{y} = \frac{1 - 2\,\beta}{\beta(2 - k)} > 0 \quad (30)$$

if $k < 2$. The situation has no meaning for $k > 2$.

If the point of intersection of the optimal curves determines the efforts of X and Y, we have

$$S^*_1 = S^*_2 = \log\left(\frac{1 - \beta k}{\beta(2 - k)}\right) - \frac{1 - 2\,\beta}{2 - k}, \quad (31)$$

which for $k = 0$ reduces to S^* of Case III of I under equal division of labor. Thus the additional motivation of imitation is, like the cooperation coefficient, a "stabilizing" influence in that a common optimum can be uniquely found.

Comparing the S^* of this case with $S_{\max}$ of Case I, we see that the imitation coefficient is sufficient motivation for cooperation if

$$D(\beta, k) \equiv S^* - S_{\max} = \log\left(\frac{1 - \beta k}{\beta(2 - k)}\right) - \frac{1 - 2\,\beta}{2 - k}$$

$$+ \log\beta - \beta + 1 > 0,$$

that is, if

$$\log\left(\frac{1-\beta k}{2-k}\right)+\frac{1-k(1-\beta)}{2-k}>0. \tag{32}$$

Let us examine the situation for stability and for conditions for complete parasitism. If X takes the initiative, he computes the behavior of Y from the second of the equations (29). Then

$$S_1=\log\left(\frac{1+k\beta x}{2\beta}\right)-\beta x, \tag{33}$$

$$\bar{x}=\frac{k-1}{k\beta}. \tag{34}$$

The condition for stability of the point $(\bar{x},\bar{y})$ determined in equations (30) is, therefore,

$$\frac{k-1}{k\beta}\geqq\frac{1-2\beta}{\beta(2-k)};$$

$$(2-k)(k-1)\geqq k-2\beta k;$$

$$(1-k)^2\leqq 2\beta k-1. \tag{35}$$

The region of stability is shown in Figure 4. From equation (34)
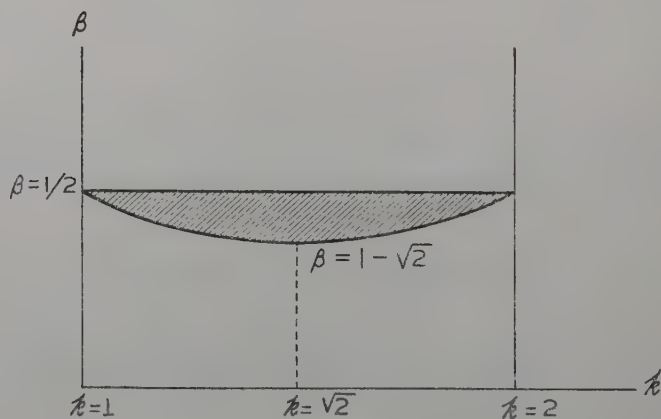
FIGURE 4

The shaded area represents the region of stability for Case IX. For the points (k,β) in the region assumption of "leadership" by X will not result in exploitation. The range of β is largest at $k=\sqrt{2}$. For smaller values of k, X will tend to exploit Y because he cannot make Y work sufficiently merely by "setting an example". For larger values of k, his own tendency to imitate Y limits the tendency to exploit.

N.B. In spite of imitative behavior in Case IX, the satisfaction function is assumed to be of the same form as in the preceding cases.

we see that parasitism occurs for $k \leqq 1$. From inequality (35) we we see that stability is insured if β is sufficiently large (provided $k > 1$, since for $k < 1$, inequality (35) can never hold, β being $< \frac{1}{2}$). Hence

Theorem 11. *Sufficient motive for cooperation under the conditions of Case IX is given by expressions (32). Parasitism does not occur for* k > 1, *and the equilibrium is stable if β is sufficiently large to satisfy inequality (35).*

Remark on Case IX. This case is peculiar in that conditions for stability are exhibited as conditions on β (provided parasitism does not occur), where a *large* value of β insures stability. An interpretation of this phenomenon can be given roughly as follows: If β is large, Y will not increase his production sufficiently when X puts the pressure on him by lowering his own production. It will pay X rather to depend on Y's imitation coefficient and have him produce by "setting an example" rather than by pressure.

Now we will discuss an inverse problem.

Case X. *Forms of satisfaction functions, from which equations (29) can be deduced.*

In the preceding case, instead of specifying a satisfaction function, we have specified the final behavior. This may be considered as a situation defining an *inverse* problem. For what forms of the satisfaction function will the given behavior be a maximizing behavior? A completely general solution is probably not interesting. It would be analogous to the problem of finding all functions of x which have a maximum at $x = \bar{x}$. But with proper restrictions the problem does yield interesting results.

We shall state the problem in the following form. Let S_1 and S_2 be given by equation (1), where R_i is a logarithmic function of a function of x and y ($R_i = \log [f(x, y)]$) and E_i is a polynomial. What change in S_i from its form given by equations (5) will result in a maximizing behavior described by equation (29)? For simplicity we let $\alpha = 0$.

Let us suppose this change is produced by two functions $z_1(x, y)$ and $z_2(x, y)$ somehow interacting with the S_i of equations (5). Even if the equations are to preserve their logarithmic-polynomial form, $z(x, y)$ can interact with the S_i of equations (5) in many different ways. It can enter as an additive term, a factor, or an exponential in the argument of the logarithm, etc., or as an additive term or a factor in E, etc. Depending on the nature of this interaction, we are led to innumerable forms of the satisfaction function, all of them leading to equations (29). While it is true, therefore, that a particular form of

the satisfaction function determines a particular form of maximizing behavior, the converse is by no means true. If at any time problems dealing with actual behavior are formulated on the basis of a maximizing behavior, it is, of course, the *behavior* which will be observed, and so the mathematical sociologist will be confronted with the ambiguous inverse problem instead of the straightforward direct one. As we shall show, however, the case is by no means hopeless. Other criteria besides the maximizing behavior enable us to accept certain of the possible forms of the satisfaction function and to reject others.

We first suppose that the change is an additive one in E:

$$S_1 = \log\left(1 + \frac{x+y}{2}\right) - \beta x + z_1(x,y),$$

$$S_2 = \log\left(1 + \frac{x+y}{2}\right) - \beta y + z_2(x,y).$$

(36)

Then

$$\frac{\partial S_1}{\partial x} = \frac{1}{2+x+y} - \beta + \frac{\partial z_1}{\partial x} = 0,$$

$$\bar{x} = \frac{1}{\beta} - y - 2 + \frac{1}{\beta}\frac{\partial z_1}{\partial x} = \frac{1}{\beta} - y - 2 + ky.$$

(37)

The general solution of the partial differential equation (37) is

$$z_1 = \beta kxy + f(y),$$

(38)

where $f(y)$ is an arbitrary function.

Similarly,

$$z_2 = \beta kxy + g(x),$$

(39)

with $g(x)$ an arbitrary function. In the simplest case $f(y) = g(x) = 0$, $z_1 = z_2 = \beta kxy$. The form of S_i is somewhat like that in Cases VII and VIII except that the xy term is added to E instead of to the argument of R. We have

$$S_1 = \log\left(1 + \frac{x+y}{2}\right) - \beta x + \beta kxy;$$

$$S_2 = \log\left(1 + \frac{x+y}{2}\right) - \beta y + \beta kxy.$$

(40)

Following the methods of the preceding sections, we could deduce analogous conditions of stability, sufficient motivation, etc. We shall not do this here, however, but instead inquire into the form of z_1 and z_2, if they are to enter as additive terms in the argument of R. (Note that if we consider z as a multiplicative factor in the argument of R, we obtain essentially the same results as in the preceding case.) We shall for convenience consider $z/2$ as the additive term. Then

$$S_1 = \log\left(1 + \frac{x + y + z_1}{2}\right) - \beta x\,;$$

$$\frac{\partial S_1}{\partial x} = \frac{1 + \dfrac{\partial z_1}{\partial x}}{2 + x + y + z_1} - \beta = 0\,;$$

$$\bar{x} = \frac{1}{\beta} - 2 - y - z_1 + \frac{1}{\beta}\frac{\partial z_1}{\partial x} = \frac{1}{\beta} - 2 - y + ky\,; \tag{41}$$

$$\frac{\partial z_1}{\partial x} - \beta z_1 = \beta k y\,. \tag{42}$$

The general solution of the partial differential equation (42) is

$$z_1 = e^{\beta x} f_1(y) - ky\,, \tag{43}$$

where $f_1(y)$ is an arbitrary function. Similarly,

$$z_2 = e^{\beta y} f_2(x) - kx\,. \tag{44}$$

In spite of the restrictions we have imposed on z_1 and z_2, we see that the solutions, being solutions of partial differential equations, are characterized by great generality. But we can further restrict the character of these solutions by additional considerations. For example, it is reasonable to demand that z_1 increase monotonically with y. Hence

$$\frac{\partial z_1}{\partial y} = e^{\beta x} f'_1(y) - k > 0 \tag{45}$$

for all values of x. Then, since only non-negative values of x are considered,

$$f'_1(y) > k\,.$$

Or we may weaken this restriction and demand that merely the part of the argument of R containing y should increase monotonically with y. Then

$$f'_1(y) > k - 1\,.$$

In the parasitic case $f'_1(y)$ can actually be negative ($k < 1$). Taking a simple function for f_1, $f_1(y) = ky$, we have

$$z_1 = ky(e^{\beta x} - 1) \geqq 0 \tag{46}$$

for all values of x and y. We might further inquire whether there exist forms of the functions $f_1(y)$ and $f_2(y)$ which would make $z_1 = z_2$, i.e., z_i symmetric in x and y. If such a form could be found, we should be dealing with a situation where the symmetric character of R_i is preserved even with the introduction of imitative behavior. It appears, however, that the functional equation $z_1(x, y) = z_2(x, y)$, where z_1 and z_2 are of the form given by equations (43) and (44), has no solutions except for $k = 0$. Hence

Theorem 11. *If imitative behavior given by equations (29) is brought about by an additive term in the argument of* R, *then* R *is not symmetric in* x *and* y.

Case XI. *Each individual desires a maximum output of the other over a period of time.*

Introducing arbitrary functions into the satisfaction function, as we have done in the inverse problem, makes it possible to impose a large variety of additional conditions. The forms of the satisfaction function we have considered in the direct problem were such that the equations

$$\frac{\partial S_1}{\partial y} = 0 \quad \text{and} \quad \frac{\partial S_2}{\partial x} = 0$$

had no solutions. The psychological interpretation of this is, of course, that it was always in the interest of one individual to have the other one work as much as possible. The negative "effort" term of X depended only on x. We could, of course, introduce many other forms of the satisfaction function which would have the effort term depend also on y and thus make possible the solution of $\dfrac{\partial S_1}{\partial y} = 0$. But which of the infinity of such satisfaction functions shall we choose?

Abstract and formal as our treatment is, we can try to keep at least a semblance of reality by deducing the forms of the satisfaction function from situations which describe an individual's interest or behavior. This we did in the inverse problem. We started with *behavior* (e.g., observed effect of increasing productivity of one individual on that of another) and deduced from it satisfaction functions determined by various forms of z. If we can consider the reluctance not a constant as we have hitherto considered it, but as a variable which is monotonically decreasing with respect to y for X and with respect to x for Y, then we have, for example,

$$\beta_1 = \beta_0 (1 - ky),$$
$$\beta_2 = \beta_0 (1 - kx). \tag{47}$$

Equations (40) then become a feasible interpretation of the observed behavior described by equation (29).

Let us now endow our individuals with a foresight. Their desires are now not so much for the maximum immediate rate of production of the other individual but for a maximum output over a period of time.

To see how such "foresight" operates, consider that X now possesses a work animal or a machine Y, which produces at a variable rate $y = y(t)$. This rate is monotonically decreasing with respect to time (because the machine is being worn out) and the rate of its decrease depends on the initial effort y_0 and on the variable effort y. This can be described by a differential equation with a boundary condition, for example,

$$y' = -y^2_0 y; \quad y(0) = y_0. \tag{48}$$

The rate of output y is now a function of t. The solution of the equation (48) is

$$y = y_0 \, e^{-y^2_0 t}. \tag{49}$$

In a unit of time $0 \leq t \leq 1$, Y will yield the total output

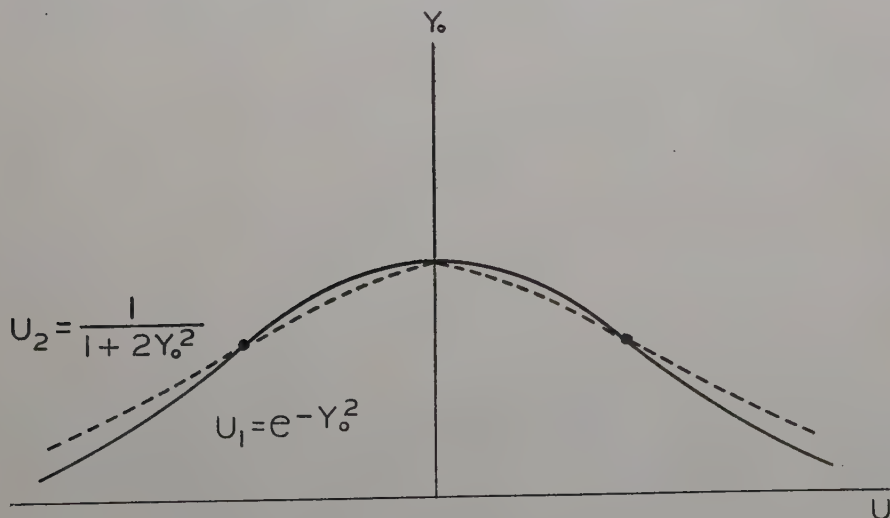$$W = \int_0^1 y\,dt = \frac{1}{y_0}(1 - e^{-y^2_0}) = W(y_0). \tag{50}$$

FIGURE 5
Graphical solution of the equation $e^{-y_0^2}(1 + 2y_0^2) = 1$.

If X wishes to maximize W with respect to the initial value of y, then differentiating with respect to y_0, we get

$$\frac{dW}{dy_0} = 1 - e^{-y_0^2} - 2y^2_0 \, e^{-y_0^2} = 0;$$ (51)

$$e^{-y_0^2}(1 + 2y^2_0) = 1.$$ (52)

An obvious root of equation (52) is $y_0 = 0$. We see, however, that this is an inflection point at $W = 0$. Another root of equation (52) exists as is readily seen by plotting

$$u_1 = e^{-y_0^2} \quad \text{and} \quad u_2 = \frac{1}{1 + 2y^2_0}.$$

(See Figure 5.) Note that for $y_0 = 0$, $u_1 = u_2 = 1$. For small positive values of y_0, $u_1 > u_2$ since

$$\frac{du_1}{dy_0} = \frac{du_2}{dy_0} = 0 \text{ at } y_0 = 0,$$

and

$$\frac{d^2u_1}{dy^2_0} > \frac{d^2u_2}{dy^2_0} \text{ at } y_0 = 0.$$

On the other hand, for large values of y_0, $u_1 < u_2$. The root of y_0 of equation (52) can be calculated from the value of u_1 where $u_1 = u_2$. This root can be shown to give a maximum W. We shall therefore call it $\bar{y}$. Similarly, we can compute $\bar{x}$, which by the symmetry of the situation equals $\bar{y}$.

We can now state the inverse problem as follows: What forms of the satisfaction function will insure

$$\left.\frac{\partial S_1}{\partial y}\right|_{y=\bar{y}} = 0;$$
$$\left.\frac{\partial S_2}{\partial x}\right|_{x=\bar{x}} = 0.$$ (53)

Finally, we can ask for the forms of the satisfaction function which will make the wishes of each individual with respect to his own and his neighbor's optimum output coincide. This is tantamount to the following conditions at the point $(\bar{x}, \bar{y})$:

$$\frac{\partial S_1}{\partial x} = \frac{\partial S_1}{\partial y} = \frac{\partial S_2}{\partial x} = \frac{\partial S_2}{\partial y} = 0,$$

$$\left(\frac{\partial^2 S_1}{\partial x\, \partial y} \right)^2 - \left(\frac{\partial^2 S_1}{\partial x^2}\, \frac{\partial^2 S_1}{\partial y^2} \right) < 0,$$

$$\left(\frac{\partial^2 S_2}{\partial x\, \partial y} \right)^2 - \left(\frac{\partial^2 S_2}{\partial x^2}\, \frac{\partial^2 S_2}{\partial y^2} \right) < 0,$$

$$\frac{\partial^2 S_1}{\partial x^2} < 0, \quad \frac{\partial^2 S_1}{\partial y^2} < 0, \quad \frac{\partial S_2}{\partial x^2} < 0, \quad \frac{\partial S_2}{\partial y^2} < 0.$$

(54)

A society of two individuals characterized by satisfaction functions which satisfy the conditions (54) would be absolutely stable in the sense that it would not be of interest to either individual to change either the rate of his own output or the rate of the other's output.

LITERATURE

Rapoport, A. 1947. "Mathematical Theory of Motivation Interactions of Two Individuals: I." *Bull. Math. Biophysics*, 9, 17–28.

A THEORY OF MEMBRANE PERMEABILITY: III.
THE EFFECT OF HYDROSTATIC PRESSURE

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Using expressions derived in previous papers, the author investigates the behavior of a cell immersed in an infinite medium, under the influence of diffusion of a single solute and flow of water. The effect of hydrostatic pressure on the system is taken into account. It is found that, depending on the values of certain parameters, the cell can collapse, burst, reach a stationary stable state, or execute undamped oscillations; a cell must burst or collapse unless its volume is an increasing function of internal pressure, and it can execute stable oscillations only if its membrane acts as a "potential well" to the molecules of the solute.

In previous publications (Bloch, 1944, 1946), equations were derived giving the permeability h (to flow of a solute) of a membrane separating two regions 0 and 1. Equation (22) of the latter paper is

$$h \equiv \frac{J}{c_0 - c_1} = \frac{D_0}{2b} \left(1 - \frac{2\phi_0}{3kT_0} \right)^{3/2} \left(1 - \frac{y - z}{u - v} \right) \frac{u \, e^{y-u} - v \, e^{z-v}}{e^{z-v} - e^{y-u}}. \quad (1)$$

The symbols are all defined in the papers cited, except for ϕ_0, which here replaces the V_0 used previously. In particular, J is defined as the flow of the solute, in grams per square centimeter of membrane per second, from region 0 into region 1; the concentrations of the solute, c_0 and c_1, and the hydrostatic pressures, P_0 and P_1, in regions 0 and 1 respectively, enter the equation through the quantities u, v, y, and z, defined below:

$$u \equiv \frac{2bH}{D_0} c_0, \qquad y \equiv \frac{2bK}{D_0} P_0,$$

$$v \equiv \frac{2bH}{D_0} c_1, \qquad z \equiv \frac{2bK}{D_0} P_1. \qquad (2)$$

Here b and D_0 are positive constants; H and K, also positive constants, are defined in terms of I, the flow of water in grams per square centimeter of the membrane per second, from region 0 into region 1:

$$I = H(c_1 - c_0) + K(P_0 - P_1)$$

$$= \frac{D_0}{2b}[(v-u) + (y-z)].$$

(3)

Equation (1) includes the effect on the motion of the solute of water flow due to both hydrostatic and osmotic pressure gradients; however, this equation has so far been applied only in the special case of equal hydrostatic pressures on the two sides of the membrane $(y = z)$. The purpose of the present paper is to investigate the more general case in which $y \neq z$.

The simplest system which seems likely to be interesting is a single cell in an infinite medium. If the interior of the cell is taken to be region 1, the equations of state of the system are

$$u = \text{const.}$$

and

$$y = \text{const.}$$

(4)

In addition, the following equations will be needed:

$$(Vv)' = AJ\frac{2bH}{D_0} = Ah(u-v),$$

(5)

and

$$V' = AI = \frac{D_0 A}{2b}(v - u + y - z).$$

(6)

Here V is the volume in the cell occupied by the solution, A is the surface area of the cell, and a prime denotes differentiation with respect to time. Equation (5) states that the rate of change of the amount of solute in the cell is equal to the rate at which solute enters the cell through the membrane; equation (6) states that the rate of increase of the volume of the cell is equal to the rate at which water enters it. Obviously equation (5) is not accurate if there is metabolism of the solute in the cell; however, the other metabolites are likely to have somewhat the same effect on water flow as the solute which is considered, and explicit treatment of more than one solute complicates the problem greatly. Equation (6) should be reasonably accurate unless the concentrations of solutes are extremely high. It will be assumed that V depends only on $z - y$, or in this case only on z; thus z' has the same sign as V' if $dV/dz > 0$, opposite sign if $dV/dz < 0$.

It will now be possible to find the equations of the curves $v' = 0$ and $z' = 0$ in the vz-plane defined by equations (4). If $v' = 0$, equations (5) and (6) combine to give

$$\frac{D_0}{2b} (v - u + y - z) \, v = h (u - v) ,\qquad (7)$$

or, from equation (1), $v' = 0$ if

$$z = v - u + y + \log \frac{1 - \beta \dfrac{u}{v}}{1 - \beta} ,\qquad (8)$$

where

$$\beta = \left(1 - \frac{2\phi_0}{3kT_0} \right)^{3/2} > 0 .\qquad (9)$$

Two cases can be distinguished: $\beta < 1$ and $\beta > 1$. These cases correspond, respectively, to the membrane's being a potential barrier and a potential well. When $\beta < 1$, equation (8) shows that v' cannot vanish for real values of z unless $v \geqq \beta u$; v' vanishes along a curve of positive slope which is asymptotic to the line $v = \beta u$ as z approaches $-\infty$ and whose slope dz/dv approaches $+1$ as v and z approach $+\infty$. When $\beta > 1$, the curve $v' = 0$ lies between the lines $v = 0$ and $v = \beta u$; as v approaches zero, z approaches $+\infty$, while as v approaches βu, z approaches $-\infty$.

The curve $z' = 0$ can be obtained on the assumption that V depends only on z and that dz/dV does not vanish for any realizable value of z. Thus $z' = 0$ when $V' = 0$, or, by equation (6), $z' = 0$ if

$$z = v - u + y .\qquad (10)$$

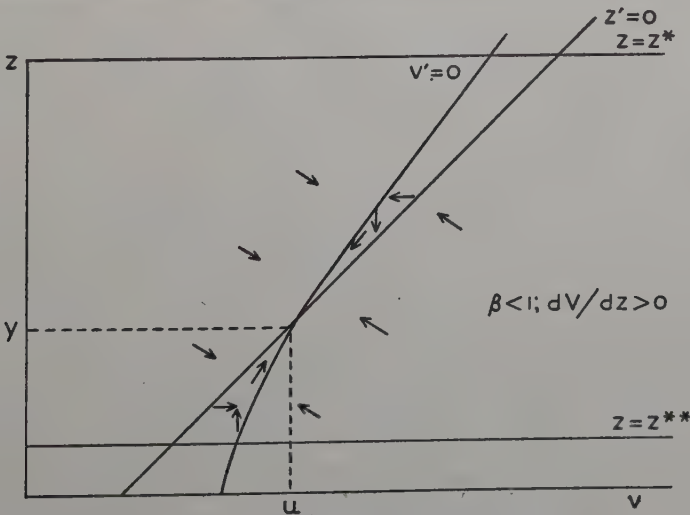This equation defines a straight line of unit slope in the vz-plane.
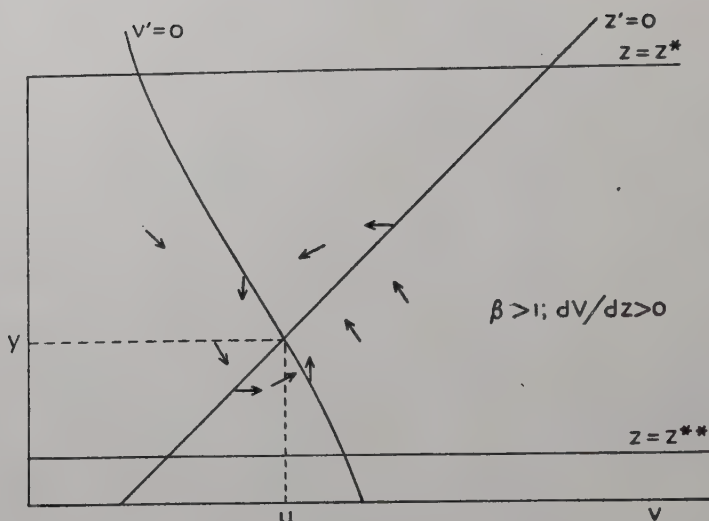

FIGURE 1

Figure 2

Figures 1 and 2 show graphs of the curves $v' = 0$ and $z' = 0$ in the first quadrant of the vz-plane (negative values of v or z are not possible). Figure 1 depicts the situation for $\beta < 1$; Figure 2, that for $\beta > 1$. For definiteness u is taken greater than y in both cases; there seems no reason to believe that the relation between u and y has any qualitative effect on the behavior of the system. In all cases the two curves $v' = 0$ and $z' = 0$ intersect at the point $v = u$, $z = y$ and nowhere else. Clearly when there is no flow of water ($z' = 0$), v' is positive when $v < u$ and is negative when $v > u$; thus $v' > 0$ to the left and $v' < 0$ to the right of the curve $v' = 0$. Also, when $v = u$, V' is negative or positive according as z is greater or less than y; $z' > 0$ to the right and $z' < 0$ to the left of the line $z' = 0$ if $dV/dz > 0$, has opposite signs if $dV/dz < 0$.

The first case to be considered is that in which V is an increasing function of z. In that case, if a representative point is on the line $z' = 0$ in either figure, its motion must be parallel to the v-axis, toward the right if the point is below and toward the left if the point is above the intersection of the two curves. If a point is on the curve $v' = 0$, its motion is parallel to the z-axis, upward if the point is below and downward if the point is above the line $z' = 0$. If a representative point is at the intersection of the curves $v' = 0$ and $z' = 0$ (i.e., at $v = u$, $z = y$), it remains there; this is the only possible stationary state for the system. A point at the right of both curves moves upward and toward the left; a point at the left of both curves moves downward and toward the right; a point between the two curves

moves upward and toward the right if it is below the line $z' = 0$, downward and toward the left if it is above that line. The situations described above are represented by the small arrows in Figures 1 and 2.

In the case being considered ($dV/dz > 0$), when $\beta < 1$, a representative point in Figure 1 which is at any time between the curves $v' = 0$ and $z' = 0$ remains between these curves and moves toward their intersection, which represents a stable configuration. A representative point which starts at the right or the left of the two curves moves toward the curves along a path of negative slope. Unless a catastrophe occurs first, the point eventually crosses one of the curves and goes to the stable point (u, y). However, there are two limiting values of hydrostatic pressure within the cell, hence two values of z: one value, $z = z^*$, corresponds to rupture of the cell membrane, while the other value, $z = z^{**}$, corresponds to collapse of the cell; or, if the cell does not collapse, z^{**} may correspond to the vapor pressure of the solution in the cell. Thus, in the case depicted, if the initial state of the system is represented by a point at the right of the two curves in Figure 1, this point ultimately reaches stability at (u, y) or else crosses the line $z = z^*$ so that the cell membrane bursts. If the representative point starts at the left of the two curves, it reaches the stable position (u, y), or else crosses the line $z = z^{**}$, so that a non-rigid cell collapses; if the cell is rigid, it may be that the internal pressure falls to the vapor-pressure of the solution in the cell (unless the constants of the membrane are changed first), so that some water-vapor is formed in the top of the cell, and water flows in the top and out the bottom keeping the internal concentration of solute at some constant value.

When $\beta > 1$, the situation is more complicated. Figure 2 shows that a representative point tends to circulate around the equilibrium position (u, y); however, it is not clear from the Figure whether such a point moves toward or away from (u, y) or, if it does approach equilibrium, how many oscillations the system executes between any given initial state and the final state. Complete answers to these questions could be found only from the solution of a differential equation which will be derived later.

However, it is possible to show by a simple argument that in some cases the system does not "blow up". Imagine a vertical straight line-segment in Figure 2, drawn upward from a point (v_1, z_1) at the right of (u, y) on the curve $v' = 0$, until it intersects the line $z' = 0$; any representative point which is initially in the region bounded by this segment and the curves $v' = 0$ and $z' = 0$ can leave this region only by crossing the line $z' = 0$. Now suppose there is a line segment

drawn from the intersection of the first segment and the line $z' = 0$ horizontally toward the left until it intersects the curve $v' = 0$ at some point (v_2, z_2) at the left of (u, y); any representative point which is initially in the region bounded by this second line segment and the curves $v' = 0$ and $z' = 0$ can leave this region only by crossing the curve $v' = 0$. The construction of line segments can be continued: a third segment can be drawn downward from (v_2, z_2) until it intersects the line $z' = 0$ at the point (v_2, z_3), and a fourth segment can be constructed toward the right from (v_2, z_3) until it intersects the curve $v' = 0$ at the point (v_3, z_3). It is clear that no representative point can cross any of these lines in the outward direction; if the point (v_1, z_1) is not between (u, y) and (v_3, z_3) on the curve $v' = 0$, a representative point that starts in the region bounded by the four line segments and the portion of the curve $v' = 0$ that lies between (v_1, z_1) and (v_3, z_3) can never leave that region. If none of the four segments intersects either of the lines $z = z^*$ and $z = z^{**}$, any system whose representative point is at any time in the region described above must either approach stability at (u, y) or eventually execute undamped oscillations about that point. If (v_1, z_1) is between (u, y) and (v_3, z_3) it is not possible to conclude from this type of reasoning that the representative point is confined to the region in question.

From the geometry of the figure it is evident that (v_3, z_3) coincides with (v_1, z_1) when $(z_2 - z_1)/(v_2 - v_1) = -1$, and is between (u, y) and (v_1, z_1) when $(z_2 - z_1)/(v_2 - v_1) < -1$. The curve $v' = 0$ lies entirely between the z-axis and the line $v = \beta u$; its slope approaches $-\infty$ as z approaches either $+\infty$ or $-\infty$; therefore, if (v_1, z_1) is far enough down the curve (perhaps below the v-axis), the average slope of the curve between (v_1, z_1) and any other point on the curve is less than -1. Thus there is in every case a finite region of the vz-plane which a representative point can never leave; obviously, however, if the smallest such region contains parts of the lines $z = z^*$ and $z = z^{**}$, the cell in question may still burst or collapse. In some cases, viz., when

$$\sqrt{\beta u} < \frac{3}{2} \tag{11}$$

the slope of the curve $v' = 0$ is everywhere less than -1, so that the construction of line segments described above will, if continued, produce a spiral curve which has (u, y) as a limit point. No representative point can cross this spiral in the outward direction; therefore, in this case any representative point that starts in such a position that it does not cross either of the lines $z = z^*$ and $z = z^{**}$ will ap-

proach stability at (u, y), though it may revolve about (u, y) several times in the process. Clearly the condition (11) is too strong; even if condition (11) does not hold, it may be that any representative point that does not cross $z = z^*$ or $z = z^{**}$ will approach (u, y). The other alternative is that its path approach some stable closed curve from either inside or outside that curve, so that the motion of the cell approaches oscillation of constant amplitude.

Some further idea of the behavior of the system may be gained from the following analysis. Equations (1), (5), and (6) imply that

$$v' = \frac{D_0 A(z)}{2bV(z)} (u - v - y + z) \left[v - \frac{u\, e^{y-u} - v\, e^{z-v}}{e^{y-u} - e^{z-v}} \right], \qquad (12)$$

and

$$z' = -\frac{D_0 A(z)}{2b\dfrac{dV}{dz}} (u - v - y + z), \qquad (13)$$

whence

$$\frac{dv}{dz} = \frac{dV}{Vdz} \left[\beta \frac{u\, e^{y-u} - v\, e^{z-v}}{e^{y-u} - e^{z-v}} - v \right]. \qquad (14)$$

Equation (14) determines the path of any representative point in terms of its initial position. However, the exact solution would be quite hard to obtain, and would very likely be too complicated to be of use. Therefore, the procedure adopted will be to reduce equations (12) and (13) to linear equations, which are approximately valid in the neighborhood of (u, y). The functions v' and z' can be expanded in Taylor series about the point (u, y):

$$v'(v, z) = v'(u, y) + (v - u)\left(\frac{\partial v'}{\partial v} \right)_{u,y} + (z - y)\left(\frac{\partial v'}{\partial z} \right)_{u,y} + \cdots,$$

and

$$z'(v, z) = z'(u, y) + (v - u)\left(\frac{\partial z'}{\partial v} \right)_{u,y} + (z - y)\left(\frac{\partial z'}{\partial z} \right)_{u,y} + \cdots.$$

$$(15)$$

These two series both converge to the functions they are being used to represent over a region of which (u, y) is an interior point. Therefore, if each series is cut off after the terms which are linear in $(v - u)$ and $(z - y)$, the values of $(v - u)$ and $(z - y)$ can be taken small enough so the series approximate the appropriate functions to any required degree of accuracy. Thus, since $v'(u, y) = z'(u, y) = 0$, the equations

$$v' = \frac{dv}{dt} = (v - u)\left(\frac{\partial v'}{\partial v}\right)_{u,y} + (z - y)\left(\frac{\partial v'}{\partial z}\right)_{u,y}$$

and   (16)

$$z' = \frac{dz}{dt} = (v - u)\left(\frac{\partial z'}{\partial v}\right)_{u,y} + (z - y)\left(\frac{\partial z'}{\partial z}\right)_{u,y}$$

can be used to investigate whether (u, y) is a position of stable or unstable equilibrium. When the derivatives in these equations are evaluated, the equations become

$$\frac{dv}{dt} = \frac{D_o A(y)}{2bV(y)}\left[(u\beta - u - \beta)(v - u) + u(1 - \beta)(z - y) \right],$$

and   (17)

$$\frac{dz}{dt} = \frac{D_o A(y)}{2b\left(\dfrac{dV}{dz}\right)_{z=y}}\left[(v - u) - (z - y) \right].$$

The solutions of these equations are

$$v = a_{11}\, e^{\lambda_1 t} + a_{12}\, e^{\lambda_2 t}$$

and   (18)

$$z = a_{21}\, e^{\lambda_1 t} + a_{22}\, e^{\lambda_2 t},$$

where the a_{ij} are constants whose values are irrelevant to the present discussion, λ_1 and λ_2 are the two quantities

$$\lambda_1, \lambda_2 = \frac{D_o A(y)}{4b}\left(\frac{dz}{dV}\right)_{z=y}\left[\psi(u\beta - u - \beta) - 1 \pm \right.$$

       (19)

$$\left. \sqrt{[\psi(u\beta - u - \beta) + 1]^2 - 4\psi(u\beta - u)} \right],$$

and ψ is the logarithmic derivative of $V(z)$ when $z = y$.

If the radicand in equation (19) is negative, the v and z coordinates of a representative point oscillate about u and y respectively; the amplitude of the oscillation increases or decreases with increasing time according as the part of λ_1 or λ_2 outside the radical is positive or negative. When $\beta > 1$, the radicand is negative if

$$\frac{1}{\psi(\beta - 1)}(\sqrt{\psi\beta} - 1)^2 < u < \frac{1}{\psi(\beta - 1)}(\sqrt{\psi\beta} + 1)^2; \quad (20)$$

if $\beta < 1$, the radicand is positive for all positive u, or oscillation of the cell can not occur, as was indicated by Figure 1. If $dV/dz < 0$,

$\psi < 0$, and there can be no oscillation; this case will be discussed later.

The quantity in front of the radical in equation (19) is positive if $\psi > 0$ and

$$u > \frac{\psi \beta + 1}{\psi (\beta - 1)} = \frac{1}{\psi (\beta - 1)} \frac{(\sqrt{\psi \beta} - 1)^2 + (\sqrt{\psi \beta} + 1)^2}{2}; \quad (21)$$

it is negative if $\psi > 0$ and the inequality sign is reversed. Thus if expressions (20) and (21) hold, the motion of the cell approaches undamped oscillation unless the representative point crosses one of the lines $z = z^*$ and $z = z^{**}$; if expression (20) but not (21) holds, the cell oscillates toward equilibrium with $v = u$ and $z = y$. The period of the oscillations in the neighborhood of (u, y) is approximately restricted by

$$\tau \gtrless \frac{4 \pi b V (y) \sqrt{\psi}}{D_0 A (y) \sqrt{\beta}} = \frac{4 \pi b \nu r}{D_0} \sqrt{\frac{\psi}{\beta}}, \quad (22)$$

where r is one of the linear dimensions of the cell when internal and external pressures are equal, and ν is the dimensionless ratio of $V(y)$ to $A(y)r$, assumed independent of y. In the case of a spherical cell, if r is the radius of the cell when internal and external pressures are equal, $\nu = \frac{1}{3}$. The period of oscillation τ has its minimum value, given by expression (22) with the equality sign, when

$$u = \frac{\psi \beta + 1}{\psi (\beta - 1)};$$

τ increases as u increases or decreases from this value, approaching infinity as u approaches either of the limits given by condition (20). Of course, expression (22) or any other relation derived from equations (16) can give at best only a very rough idea of the period of any oscillation that may occur far from the point (u, y).

When $\beta < 1$ or $\psi < 0$, or when condition (20) is not satisfied, the solutions of equations (16) are not oscillatory, or the motion of a representative point is not oscillatory in the immediate neighborhood of (u, y) where equations (16) are approximately valid. However, if (u, y) is not a position of stable equilibrium, that is, when inequality (21) is satisfied, and $\beta > 1$ and $\psi > 0$, the straight line construction described above shows that the representative point has a stable closed path around (u, y) on which its motion is oscillatory, whether or not there is oscillation in the immediate neighborhood of (u, y). Thus expression (21) is the condition for the existence of

stable oscillations of the cell, and when condition (21) is not satis-
fied, β being greater than unity and dV/dz being positive, the cell
approaches a stationary state in which hydrostatic pressure and so-
lute concentration are each the same inside as outside. Incidentally,
as is to be expected, the very strong condition (11) implies that weak-
er condition (21) does not hold. It will be recalled that when $\beta < 1$
and $dV/dz > 0$ the cell always approaches the stationary state. The
foregoing remarks apply, of course, only if in the process of approach-
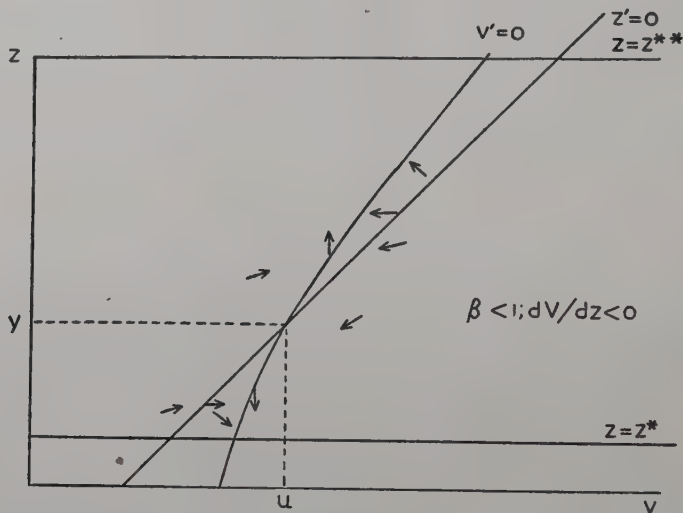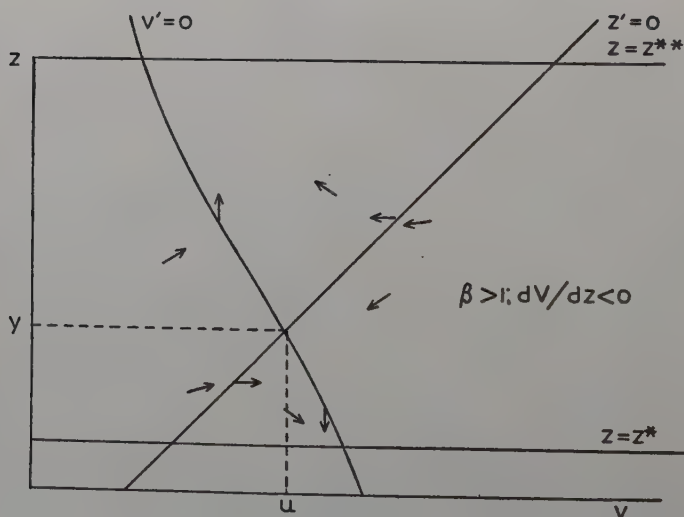ing the final state the cell does not burst or collapse.

FIGURE 3

FIGURE 4

When $dV/dz < 0$, the situation is as depicted in Figure 3 ($\beta < 1$) and Figure 4 ($\beta > 1$); here z^{**}, corresponding to collapse of the membrane, is greater than z^*, corresponding to rupture of the membrane. At any given point in one of these Figures, the sign z' is opposite to its sign at the corresponding point in Figures 1 and 2. Figures 3 and 4 show that a cell whose membrane is such that $dV/dz < 0$ must either explode or collapse.

Finally, a few remarks will be made about the relation between the function $V(z)$ and the tension of the cell membrane. If the shape of the cell is independent of the volume, conservation of energy during a small change of volume implies that

$$(P_1 - P_0)\,dV = \frac{D_0}{2bK}\,(z - y)\,dV = \sigma(V)\,dA = \delta\,\sigma(V)\,V^{-1/3}\,dV, \quad (23)$$

where $\sigma(V)$ is the tension in the cell membrane, in general a function of the area and hence of the volume, and δ is defined as

$$\delta \equiv \frac{3}{2}\frac{V^{2/3}}{A},$$

a constant if the shape of the cell is invariant. For a spherical cell, δ has the value $\frac{1}{2}(4\pi/3)^{-1/3}$. Equation (23) states that the work done by hydrostatic pressure in changing the volume of the cell is equal to the work done against the membrane tension in changing the area of the membrane. It implies that

$$z - y = \frac{2bK\delta}{D_0}V^{-1/3}\,\sigma(V).$$

It seems reasonable to suppose that $\sigma(V)$ is either constant (as in the case of the surface tension of a drop of liquid) or else a monotonically increasing function of V. If $\sigma(V)$ is the n-th power of V, then, when $z = y$, V is either zero or infinity depending on whether n is greater or less than $\frac{1}{3}$; thus, if $dV/dz > 0$ ($n > \frac{1}{3}$), the cell is collapsed when $z = y$, or every such cell must collapse if it does not burst first, while if $dV/dz < 0$ ($n < \frac{1}{3}$), the membrane is ruptured when $z = y$. Therefore, $\sigma = V^n$ is not a possible condition for a durable cell. The quantity $\sigma(V)$ must, in addition to being an increasing function, have a root at some value of V, $V_0 = V(y) \neq 0$; furthermore, σ must increase rapidly enough so that $dz/dV > 0$, if the cell is to survive. A simple possible form for $\sigma(V)$ is $C(V - V_0)^n$, where n is an odd positive integer and C is a constant. The rapidity with which $\sigma(V)$ increases is a measure of the rigidity of the cell membrane, as is the reciprocal of the quantity ψ used above.

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THE MECHANISM OF THE MIDDLE EAR:
PART II. THE DRUM

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The ear drum is considered to be a thin circular membrane with radial and circular fibers, whose center is pulled inwards by the handle of the hammer. It is shown that such a membrane is equivalent to a rigid piston connected by a lever to the handle of the hammer, and subjected to elastic forces. The stability of the equivalent system is great, and the flexibility of the lever is very small. The lever is such that small pressures in the auditory canal are transformed into larger forces on the hammer. The leverage ratio increases with the tension of the tensor tympani and decreases with the number of circular fibers.

Method. We shall proceed as follows: We first derive the equations of equilibrium of the drum, and find the shape of its meridian, when subjected to a force ϕ on its center and a uniform pressure p on one of its sides. We consider next a small change $\Delta\phi$ of the force and Δp of the pressure, and study the corresponding deformation of the drum and the variation of its tension. Neglecting all infinitesimals of second order, we obtain linear relations between the various increments Δ. From these relations we eliminate all variables relating only to internal characteristics of the drum, and so obtain equations relating the force on the hammer and its motion to the pressure and motion of the air in the auditory canal. These equations are:

$$\Delta\phi = - K\pi R^2 \Delta p - A \Delta X,$$

$$\Delta X = \frac{1}{K} \frac{\Delta V}{\pi R^2} - B\pi R^2 \Delta p. \tag{1}$$

They show that the force $\Delta\phi$ on the handle of the hammer depends linearly on the force $\pi R^2 \Delta p$ exerted by the air on the drum, and on the displacement ΔX of the hammer, and that the displacement ΔX depends linearly on the average displacement $\Delta V/\pi R^2$ of the drum, and on the force $\pi R^2 \Delta p$ transmitted. The equations (1) indicate that the drum is equivalent to a system formed by a rigid piston, a flexible lever, and a spring which opposes displacements of the lever from its position of equilibrium. The quantity K is the ratio

of the two lever arms, A is the stiffness of the spring, and B measures the flexibility of the lever arms.

Under very particular assumptions, which were originally made by H. Helmholtz (1873), we find easily the value of the coefficient K, and find also that $B = 0$. Under more general assumptions however, the coefficients K, A, B appear first as complicated expressions, and several sections of this paper will deal with the simplifications of these expressions.

Anatomical description of the drum. The ear drum is a thin circular membrane (its thickness is 1/10 mm and the ratio of its smallest radius to its largest radius is about 4/5). It is tightly stretched over a perforation of the temporal bone, and its center is pulled inward by the handle of the hammer ossicle, which itself is pulled inward by ligaments and by a muscle, the "tensor tympani". The intensity of this pull varies, mainly in animals, with the loudness of the sound transmitted. The handle may be considered to be attached to the drum at one point because, although in reality the handle is attached to the drum all along one radius, the pulling force by the handle seems to be concentrated at the center of the drum. The drum consists of two layers of tendon-like collagenous fibers and is covered on both sides by an epithelial layer. The fibers on the side of the outer ear are radial and the fibers on the side of the middle ear are circular. The radial fibers are curved, which indicates that the circular fibers are tense. The circular fibers are most numerous towards the periphery.

A small region of the drum, called "pars flaccida", lacks fibers and is therefore slack. Its existence implies that the fibers do not have a strictly radial, circular arrangement and that the air pressure in the auditory canal is not always exactly what it would be if the entire drum were under tension. The effect of the pars flaccida will be neglected in our calculations. For a further description of the drum, see, for instance, F. R. Bailey (1936, p. 573).

Notations. We shall use the following notations:

$x =$ abscissas, measured on the axis of revolution of the drum, with positive direction toward the outer ear,

$r =$ ordinates of the meridian of the drum, or radii of the circular fibers,

$\alpha = \alpha(r) =$ angle, at a variable point, of the meridian with the x axis,

$s = s(r) =$ arc length,

$R =$ radius of the circle of attachment of the drum to the temporal bone,

$X = x(R) - x(0)$, $S = s(R) - s(0)$, $a_o = a(0)$,

$\gamma_r = \gamma_r(r) =$ tension in the direction of the radial fibers,

$\gamma_c = \gamma_c(r) =$ tension in the direction of the circular fibers,

$\Gamma = \Gamma(r) = 2\pi r \gamma_r(r) =$ total tension, along one parallel, of all the radial fibers,

$\phi =$ pull of the hammer on the drum,

$p =$ excess of air pressure in the outer ear over the pressure in the middle ear.
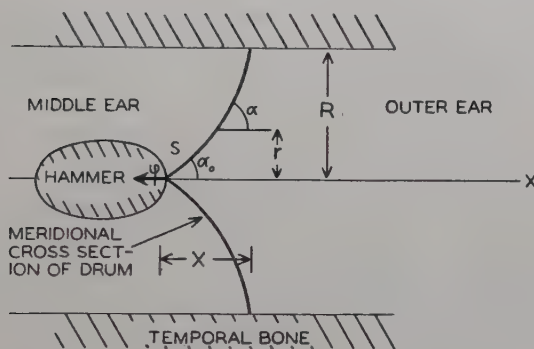
FIGURE 1

Equation of equilibrium of the drum. We consider the portion of drum limited by a circular fiber of radius r . This portion is in equilibrium under the pull ϕ of the hammer, the resultant $\Gamma \cos \alpha$ of the radial fibers along the parallel r and the force $\pi r^2 p$ exerted by the air. We have, therefore,

$$\phi + \pi r^2 p = \Gamma \cos \alpha = 2\pi r \gamma_r \cos \alpha . \tag{2}$$

We consider an elementary surface of the drum contained between two circular fibers of radius r and $r + dr$ and between two meridional planes forming an angle $d\theta$. We obtain two equations of equilibrium by writing that this element of the drum is in equilibrium first with respect to forces tending to move it in the tangential direction and second with respect to forces tending to move it in a direction normal to the surface. The two forces acting tangentially on the

two arcs of parallel are $\gamma_r r d\theta$ and $(\gamma_r + d\gamma_r)(r + dr)d\theta = \gamma_r r d\theta + d(\gamma_r r)d\theta$. The two forces acting on the two arcs of meridian are $\gamma_c ds$. They form an angle $\pi - d\theta$, and have, therefore, a resultant equal to $\gamma_c ds\, d\theta$. This resultant is directed along the radius. Its projection on the tangential plane is $\gamma_c\, ds\, d\theta \sin \alpha = \gamma_c\, dr\, d\theta$. Since this projection equals the tangential resultant $d(\gamma_r r)d\theta$ of the forces on the arcs of parallels, we obtain

$$\gamma_c = \frac{d(r\,\gamma_r)}{dr} = \frac{1}{2\pi}\frac{d\Gamma}{dr}. \tag{3}$$

The condition of equilibrium with respect to the forces normal to the surface leads towards the known equation

$$p = \frac{\gamma_r}{\rho_r} + \frac{\gamma_c}{\rho_c},$$

where ρ_r and ρ_c are the two principal radii of curvature of the surface. These radii are positive if the corresponding centers of curvature are in the region containing the fluid under pressure p, and negative in the contrary case. We have

$$\rho_r = -\frac{ds}{d\alpha} = -\frac{dr}{\sin \alpha\, d\alpha} = \frac{dr}{d\cos \alpha}.$$

Two normals to the membrane at two points of a same parallel intersect on the axis of revolution. Therefore $\rho_c = r/\cos \alpha$. We thus obtain the equation

$$p = \gamma_r \frac{d\cos \alpha}{dr} + \gamma_c \frac{\cos \alpha}{r}. \tag{4}$$

The three equations (2), (3), and (4) are not independent, and equation (4) is a consequence of equations (2) and (3).

Equation of the meridian. We have thus far two independent equations, namely, equations (2) and (3), to determine the three unknown functions $r(x)$, $\gamma_r(r)$, $\gamma_c(r)$. A third equation is required. This equation depends on the relative distribution and tension of the circular fibers, and must therefore be obtained by considerations other than purely static.

If the shape of the drum is given by an equation $r = r(x)$, then we obtain successively $\alpha(r)$ by $\tan \alpha = dr/dx$, $\gamma_r(r)$ by equation (2), and $\gamma_c(r)$ by equation (3).

Conversely, if the function $\gamma_c(r)$ is given, then we obtain $\gamma_r(r)$ from equation (3), which we write in the form

$$r\gamma_r = \frac{\Gamma}{2\pi} = \int_0^r \gamma_c(r)\, dr + a, \tag{5}$$

a being a constant of integration. The function $a(r)$ is then obtained from equation (2) and the function $x(r)$ is obtained from

$$x(r) = \int_0^r \frac{dr}{\tan a} = \int_0^r \frac{(\phi + \pi\, pr^2)\, dr}{\sqrt{\Gamma^2 - (\phi + \pi\, pr^2)^2}}. \tag{6}$$

If γ_c is given as a function of s instead of as a function of r, and if $p = 0$, we use the following expression:

$$\gamma_c = \frac{1}{2\pi}\frac{d\Gamma}{dr} = \frac{1}{2\pi\sin a}\frac{d}{ds}\frac{\phi}{\cos a}$$

$$= -\frac{\phi}{2\pi}\frac{1}{\sin a \cos^2 a}\frac{d}{ds}\cos a = \frac{\phi}{2\pi\cos^2 a}\frac{1}{ds}\frac{da}{ds} = \frac{\phi}{2\pi}\frac{d\tan a}{ds}.$$

Therefore,

$$\tan a = \frac{2\pi}{\phi}\int_0^s \gamma_c(s)\, ds + \tan a_0. \tag{7}$$

We thus obtain $\tan a = dr/dx$ as a function of s. The functions $x(s)$ and $r(s)$ are then obtained from

$$x = \int_0^s \frac{i\, ds}{\sqrt{1 + \tan^2 a}}, \quad r = \int_0^s \frac{\tan a}{\sqrt{1 + \tan^2 a}}\, ds.$$

Case where γ_c is constant and p is zero. We shall apply to this particular case the results of the preceding section. Defining two constants b and c by

$$b = \gamma_c, \quad c = \phi/(2\pi b),$$

the equations (5), (2), (7), and (6) give respectively:

$$r\gamma_r = \frac{\Gamma}{2\pi} = a + br, \cos a = \frac{bc}{a + br}, \tan a - \tan a_0 = cs,$$

$$x = \int_0^r \frac{bc\, dr}{\sqrt{(a + br)^2 - b^2 c^2}} = c \arg\cosh \left. \frac{a + br}{bc}\right|_0^r.$$

Thus the meridian appears to be a hyperbolic cosine curve. For such curves we have the following known relations, d being a suitable constant:

$$r + \frac{a}{b} = c \cosh \frac{x+d}{c} = \sqrt{s^2 + c^2} = \frac{c}{\cos \alpha},$$

$$\frac{dr}{dx} = \sinh \frac{x+d}{c} = \frac{s}{c} = \tan \alpha, \tag{8}$$

$$\log \left[r + \frac{a}{b} + \sqrt{\left(r + \frac{a}{b}\right)^2 - c^2} \right] - \log A = \frac{x+d}{c} = \log \frac{1 + \sin \alpha}{\cos \alpha}.$$

The condition that these equations have a meaning for $r = 0$ requires that $a \geqq bc = \phi/2\pi$.

The case where we take as the third equation $\gamma_c(r) = \gamma_r(r)$ instead of $\gamma_c(r) = b$ is of interest because the condition $\gamma_c = \gamma_r$ is characteristic of amorphous surfaces or surfaces with random disposition of fibers (such as rubber membranes) and also of surfaces of minimal area. In that case, equation (3) gives $\gamma_c = \gamma_r + d\gamma_r/dr$. Therefore, the equation $\gamma_c = \gamma_r$ implies that γ_r, and therefore also γ_c, is a constant. It follows that equations (8) are again valid, and that $a = 0$. Since for $a = 0$ equations have a meaning only for $r \geqq c$, it is necessary to suppose that the attachment of the hammer to the drum is circular and has a radius at least equal to c.

The hypotheses of Helmholtz. H. Helmholtz (1873, appendix) makes the following three hypotheses:

1. The shape of the drum is the one it would have if there were no circular fibers but if there were instead an additional pressure q in the middle ear.
2. The radial fibers are inextensible, which means that their length is independent of their tension.
3. The circular fibers are extensible, which implies that their tension changes only when their length changes.

The interest of these hypotheses will be seen in the following section. In the present section we shall determine the functions $\alpha(r)$, $x(r)$, $\gamma_r(r)$ and $\gamma_c(r)$ resulting from the first hypothesis.

From assumption (1) we obtain $\alpha(r)$ and $x(r)$ by setting $\gamma_c = 0$ in equation (5) and $p = -q$ in equations (2) and (6):

$$\cos \alpha(r) = \frac{\phi - \pi r^2 q}{2\pi a} = \cos \alpha_0 \left(1 - \pi r^2 q/\phi\right),$$

(9)

$$x(r) = \int_0^r \frac{\phi - \pi q r^2}{\sqrt{(2\pi a)^2 - (\phi - \pi q r^2)^2}} \, dr.$$

This is an elliptic integral. H. Helmholtz (1873, pp. 67-69) studied this integral and gives a figure of the meridian for $\alpha_0 = 40°$.

Actually, however, $\gamma_c \neq 0$ and $p = 0$. Helmholtz's first hypothesis amounts to the assumption that equations (9) hold. We obtain $\gamma_r(r)$ and $\gamma_c(r)$ from equations (2) and (3):

$$2\pi r \gamma_r = \Gamma = \frac{\phi}{\cos \alpha} = \frac{\phi}{\cos \alpha_0} \frac{1}{1 - \pi r^2 q/\phi},$$

(10)

$$\gamma_c = \frac{1}{2\pi} \frac{d\Gamma}{dr} = \frac{1}{\cos \alpha_0} \frac{qr}{(1 - \pi r^2 q/\phi)^2}.$$

The last equation agrees with the observation that the density of the circular fibers increases towards the periphery of the drum.

Transmission of forces under the Helmholtz hypotheses. The Helmholtz hypotheses lead towards some simple conclusions, because they enable us to study different conditions of equilibrium without considering deformations of the drum. We shall show that the position of equilibrium of the drum does not depend on the pressure in the auditory canal as long as there is no displacement of the hammer.

Let us consider a pressure Δp in the auditory canal. Leaving the function $\alpha(r)$ unchanged, we increase all stresses and the pull on the hammer by amounts equal to $-\Delta p/q$ times their values when there is an excess of pressure q in the middle ear, but no circular tension. Then the equations (2), (3) and (4) of equilibrium of the drum, being linear and homogeneous in γ_r, γ_c, ϕ and p, remain satisfied for the new state of the drum, and the equations of elasticity of the fibers are also satisfied, for we have no change in the length of the radial fibers, and no change in length and tension of the circular fibers. We have, therefore, a new state of equilibrium. The first Helmholtz hypothesis was made in order to have the increments of the different forces satisfy the linear equations (2), (3) and (4), the second hypothesis in order to avoid a stretching of the radial fibers due to the increase of their tension, and the third hypothesis was necessary in order to have the values of the tensions determined uniquely.

In particular, the increment $\Delta\phi$ of the pull ϕ in the new state is

$$\Delta\phi = -\frac{\Delta p}{q}\,\phi = -\frac{\phi}{\pi R^2 q}\,\pi R^2 \Delta p. \tag{11}$$

Thus to a force $\pi R^2 \Delta p$ exerted by the air on the drum corresponds a force $-\Delta\phi$ exerted on the hammer, which is $\phi/(\pi R^2 q)$ times larger. Therefore, for transmission of forces without motion, the drum is equivalent to a piston connected to the hammer by a lever increasing forces in the ratio

$$K = \frac{\phi}{\pi R^2 q} = \frac{\text{force of pull}}{\text{force of pressure}}. \tag{12}$$

This lever is rigid [$B = 0$ in equation (1)] because for an immobilized hammer there is no motion of the drum whatever the force acting on it. The ratio K can be made as large as we want by making q, and therefore the circular tension γ_c [cf. equation (10)], small enough. The ratio K can in particular have the value 3 or 4, which was found to be most suitable for the ear (Esser, 1947). The ratio K depends on ϕ. Therefore the efficiency of the ear can be modified by changing the tension of the tensor tempani.

Displacement of the drum; discussion of the hypotheses. The preceding sections gave the essential properties of a non-moving drum. In the following we shall study displacements of the drum from its position of rest. No assumption will be made about the distribution of the circular fibers. In other words, the function $\gamma_c(r)$ will remain indeterminate. We shall, however, suppose that the circular stress $\gamma_c(r)$ does not change during the motions of the drum. This assumption is made for mathematical simplification, but is not justified by physical or anatomical considerations. It would be justified

1) if the elongation of the circular fibers were small in comparison to the elongation of the radial fibers (movements parallel to the x axis),

2) or if the circular fibers were very stretchable, in the sense that small changes in tension were to induce large elongations.

Our hypothesis is to some extent similar to Helmholtz's hypotheses (2) and (3) in the sense that it supposes the circular fibers much more extensible than the radial fibers, but with the emphasis on the extensibility of the circular fibers rather than on the inextensibility of the radial fibers. As far as we know, no such difference of elasticity of the two sets of fibers has been observed in the living ear.

We shall use the notations $\gamma(r)$, $x(r)$, $\alpha(r)$, ϕ, $p = 0$, etc., to

denote functions and quantities relative to the rest position and will designate the same functions or quantities by $\gamma(r) + \Delta\gamma(r)$, $x(r) + \Delta x(r)$, $a(r) + \Delta a(r)$, $\phi + \Delta\phi$, Δp, etc., at an arbitrary moment. We suppose that all increments Δ are small enough to allow us to neglect terms of the second order and therefore we can apply all the rules of differential calculus to the increments Δ.

As we have $p = 0$ and $\Delta\gamma_c(r) = 0$, we obtain from equations (2) and (5):

$$\Gamma \cos a = \phi, \tag{13}$$

$$\Delta \Gamma = 2\pi \Delta a = \text{constant.} \tag{14}$$

Thus $\Delta\Gamma$ is independent of r.

Displacement of the hammer. In this section, we shall calculate the displacement $- \Delta X$ of the hammer in terms of $\Delta\phi$, Δp and $\Delta\Gamma$. We have $X = \int_0^R dr/\tan a$, therefore,

$$\Delta X = \int_0^R \Delta \frac{1}{\tan a} \, dr. \tag{15}$$

We have also

$$\Delta \frac{1}{\tan a} = - \frac{\Delta a}{\sin^2 a} = \frac{\Delta \cos a}{\sin^3 a}, \tag{16}$$

and, from equation (2), we obtain

$$\Delta \cos a = \Delta \frac{\phi + \pi r^2 p}{\Gamma} = \frac{\cos a}{\phi} (\Delta\phi + \pi r^2 \Delta p) - \frac{\cos^2 a}{\phi} \Delta\Gamma. \tag{17}$$

We introduce the following notations, some of which will be used now and some of which will be used in later sections:

$$L = \int_0^R \frac{\cos a}{\sin^3 a} \, dr, \quad M = \int_0^R \frac{\cos^2 a}{\sin^3 a} \, dr, \quad N = \int_0^R \frac{\cos^3 a}{\sin^3 a} \, dr,$$

$$P = \frac{1}{R^2} \int_0^R \frac{\cos a}{\sin^3 a} \, r^2 dr, \quad Q = \frac{1}{R^2} \int_0^R \frac{\cos^2 a}{\sin^3 a} \, r^2 dr, \tag{18}$$

$$T = \frac{1}{R^4} \int_0^R \frac{\cos a}{\sin^3 a} \, r^4 dr.$$

Expressions (18), together with equations (15), (16), (17), give

$$\Delta X = \frac{\Delta \phi}{\phi} L + \frac{\pi R^2 \Delta p}{\phi} P - \frac{\Delta \Gamma}{\phi} M. \tag{19}$$

Calculation of arc length and volume. We calculate now the increase ΔS of the length of the radial fibers in terms of $\Delta \phi$, Δp, $\Delta \Gamma$. We have $S = \int_0^R dr/\sin \alpha$, therefore,

$$\Delta S = \int_0^R \Delta \frac{1}{\sin \alpha} dr,$$

$$\Delta \frac{1}{\sin \alpha} = \frac{\cos \alpha \, \Delta \cos \alpha}{\sin^3 \alpha}. \tag{20}$$

Thus the integrand in equation (20) differs from the integrand in equation (15) by a factor $\cos \alpha$. Therefore, ΔS is obtained by replacing in the second member of equation (19) the integrals L, P, M, by M, Q, N respectively. We thus obtain

$$\Delta S = \frac{\Delta \phi}{\phi} M + \frac{\pi R^2 \Delta p}{\phi} Q - \frac{\Delta \Gamma}{\phi} N. \tag{21}$$

We now calculate the increase ΔV of the volume of air contained in the auditory canal. The quantity $\Delta V/(\pi R^2)$ measures the average displacement of the drum or the displacement of a rigid piston equivalent to the drum. We have

$$V = \pi \int_0^X r^2(x) \, dx = \pi \int_0^R \frac{r^2}{\tan \alpha} dr,$$

$$\Delta V = \pi \int_0^R r^2 \Delta \frac{1}{\tan \alpha} dr.$$

The integrand in this equation differs from the integrand in equation (15) by a factor r^2. Therefore, $\Delta V/\pi$ is obtained by replacing in the second member of equation (19) the integrals L, P, M by $R^2 P$, $R^2 T$, $R^2 Q$ respectively. We thus obtain

$$\frac{\Delta V}{\pi R^2} = \frac{\Delta \phi}{\phi} P + \frac{\pi R^2 \Delta p}{\phi} T - \frac{\Delta \Gamma}{\phi} Q. \qquad (22)$$

Elimination of $\Delta \Gamma$. We shall find the relation existing between ΔS, $\Delta \Gamma$ and the coefficient k of elasticity of the radial fibers. This relation will enable us to eliminate $\Delta \Gamma$ from equations (19) and (22).

The coefficient k of elasticity of a fiber is defined by $\Delta \gamma / \gamma = k \Delta s / s$, where γ indicates the tension at rest of an element of fiber of length s and $\gamma + \Delta \gamma$ indicates the tension of the same element when it is stretched to the length $s + \Delta s$.

The increase ΔS of the length of a radial fiber for a given value of $\Delta \Gamma$ is calculated as follows:

$$\Delta S = \int_0^s \frac{1}{k} \frac{\Delta \gamma_r}{\gamma_r} ds = \frac{\Delta \Gamma}{k} \int_0^s \frac{ds}{\Gamma}$$

$$= \frac{\Delta \Gamma}{k} \int_0^s \frac{\cos \alpha}{\phi} ds = \frac{\Delta \Gamma}{k \phi} \int_0^x dx;$$

$$\Delta S = \frac{X}{k \phi} \Delta \Gamma. \qquad (23)$$

This is the desired relation between ΔS and $\Delta \Gamma$. Elimination of ΔS from equations (21) and (23) gives

$$\frac{\Delta \Gamma}{\phi} \left(N + \frac{X}{k} \right) = \frac{\Delta \phi}{\phi} M + \frac{\pi R^2 \Delta p}{\phi} Q. \qquad (24)$$

Substitution into equation (19) gives

$$\Delta X \left(N + \frac{X}{k} \right) = \frac{\Delta \phi}{\phi} \left[\frac{X}{k} L + NL - M^2 \right]$$

$$+ \frac{\pi R^2 \Delta p}{\phi} \left[\frac{X}{k} P + NP - MQ \right].$$

Solving the preceding equation for $\Delta \phi$, we obtain

$$\Delta \phi = - K \pi R^2 \Delta p + A \Delta X, \qquad (25)$$

where

$$K = \frac{(X/k) P + NP - MQ}{(X/k) L + NL - M^2}, \quad A = \frac{X/k + N}{(X/k) L + NL - M^2} \phi. \qquad (26)$$

This proves the validity of the first equation (1).

Elimination of $\Delta\phi/\phi$ and $\Delta\Gamma/\phi$ from equations (19), (24) and (22) gives, in the form of a determinant,

$$\begin{vmatrix} L & M & -\Delta X + P\pi R^2 \Delta p/\phi \\ M & N + X/k & Q\pi R^2 \Delta p/\phi \\ P & Q & -\Delta V/\pi R^2 + T\pi R^2 \Delta p/\phi \end{vmatrix} = 0 .$$

Expanding this determinant, we obtain

$$\Delta X = \frac{1}{K} \frac{\Delta V}{\pi R^2} - B\pi R^2 \Delta p , \qquad (27)$$

where K has the value given by equation (26) and where

$$B = \frac{(X/k)(LT - P^2) + D}{(X/k)P + NP - MQ} \frac{1}{\phi}; \quad D = \begin{vmatrix} L & M & P \\ M & N & Q \\ P & Q & T \end{vmatrix} . \qquad (28)$$

By establishing equation (27), we prove also the validity of the second equation (1). An interpretation of these equations (1) in terms of an equivalent mechanical system has been given in the first section. It should be remembered from our definitions that ΔX or ΔV are positive when the hammer or the drum move toward the middle ear, which is in the negative x direction.

Introduction of multiple integrals. In the coefficients K, A, B in equations (25) and (27) appear the four determinants:

$$\begin{vmatrix} N & M \\ Q & P \end{vmatrix} , \quad \begin{vmatrix} L & M \\ M & N \end{vmatrix} , \quad \begin{vmatrix} L & P \\ P & T \end{vmatrix} \text{ and } D = \begin{vmatrix} L & M & P \\ M & N & Q \\ P & Q & T \end{vmatrix} . \qquad (29)$$

We shall transform the three first determinants into double integrals and the determinant D into a triple integral. These multiple integrals will be used in later sections to find the order of magnitude of the determinants for small values of $\alpha(R) - \alpha(0)$, to calculate their approximate values and to find the range of possible values of K.

We define a function $u(r)$ by

$$u(r) = \int_0^r \frac{\cos \alpha}{\sin^3 \alpha} dr . \qquad (30)$$

This function $u(r)$ is monotonically increasing, and therefore the inverse function $r(u)$ is well defined and monotonic. We use also the notation

$$c(u) = \cos \alpha[r(u)] . \qquad (31)$$

Then the integrals (18) become

$$L = \int_0^L du, \quad M = \int_0^L c(u)\,du, \quad N = \int_0^L c^2(u)\,du,$$

$$P = \frac{1}{R^2}\int_0^L r^2(u)\,du, \quad Q = \frac{1}{R^2}\int_0^L r^2(u)\,c(u)\,du, \quad T = \frac{1}{R^4}\int_0^L r^4(u)\,du. \tag{32}$$

We have

$$\int_0^L \int_0^L [c(u) - c(v)]$$

$$\cdot [c(u)\,r^2(v) - c(v)\,r^2(u)]\,du\,dv = 2R^2(NP - MQ), \tag{33}$$

because, multiplying out the integrand, we find

$$\int_0^L c^2(u)\,du \int_0^L r^2(v)\,dv - \int_0^L c(u)\,r^2(u)\,du \int_0^L c(v)\,dv$$

$$- \int_0^L c(u)\,du \int_0^L c(v)\,r^2(v)\,dv + \int_0^L r^2(u)\,du \int_0^L c^2(v)\,dv$$

$$= N(PR^2) - (QR^2)M - M(QR^2) + (PR^2)N = 2R^2(NP - MQ).$$

By a similar argument, we obtain the formulae

$$2(LN - M^2) = \int_0^L \int_0^L [c(u) - c(v)]^2\,du\,dv, \tag{34}$$

$$2R^4(LT - P^2) = \int_0^L \int_0^L [r^2(u) - r^2(v)]^2\,du\,dv, \tag{35}$$

$$R^4 D = \int_0^L \int_0^L \int_0^L [c(u) - c(v)][c(v)\,r^2(w) - c(w)\,r^2(v)]$$

$$\cdot [r^2(u) - r^2(w)]\,du\,dv\,dw. \tag{36}$$

Thus we have expressed in equations (33), (34), (35) and (36) the determinants (29) as multiple integrals. The integrands in equa-

tions (33), (34) and (35) are positive; therefore the first three determinants (29) are positive.

Magnitudes for small $\alpha(r) - \alpha(0)$. As in the case of Helmholtz's hypotheses, it will be found that $\alpha(r) - \alpha(0)$ must be small in order to obtain a large value of K. When $\alpha(r) - \alpha(0)$ is small, the determinants (29) appear as differences of approximately equal terms, and are therefore inconvenient to use. However, the multiple integrals are of such a form that their magnitude can be estimated.

The integrands in equations (33), (34), and (35) have the same (positive) sign over the whole domain of integration. Therefore, the corresponding integrals have the same order of magnitude as their integrands. For small values of $\alpha(r) - \alpha(0)$, the difference $c(u) - c(v)$ is an infinitesimal of first order, while $c(u)r^2(v) - c(v)r^2(u)$ and $r^2(u) - r^2(v)$ are not small. Consequently, $LT - P^2$ is not small, $NP - MQ$ is an infinitesimal of first order, and $LN - M^2$ is an infinitesimal of second order in $\alpha(R) - \alpha(0)$.

The determinant D is an infinitesimal of at least first order in $\alpha(R) - \alpha(0)$, but as the integrand in equation (36) does not remain positive, D may be an infinitesimal of higher order. We shall show that it is at least of second order.

We have

$$\int_0^L \int_0^L \int_0^L [c(u) - c(v)][r^2(w) - r^2(v)]$$

$$\cdot [r^2(u) - r^2(w)]\, du\, dv\, dw = 0 , \tag{37}$$

because the integrand is an odd function of $u - v$ and the domain of integration is symmetric in u and v. We multiply the two members of the preceding equation by an arbitrary constant A and subtract from equation (36). We thus find that equation (36) remains valid when we replace the integrand by

$$[c(u) - c(v)][\{c(v) - A\} r^2(w)$$

$$- \{c(w) - A\} r^2(v)][r^2(u) - r^2(v)].$$

If we now take for A an average value of $c(v)$, it becomes evident that the integrand is an infinitesimal of at least second order in $\alpha(R) - \alpha(0)$.

We shall now find the range of possible values of the ratio K, defined by equation (26). The denominator of K is positive for all values of the coefficient of elasticity k. As k varies from zero to infinity, K varies continuously and monotonically from the value P/L to the value $(NP - MQ)/(NL - M^2)$. The value P/L approximately

equals 1/3, as is seen by taking u proportional to r in formulas (32). The value $(NP - MQ)/(NL - M^2)$ can be made as large as we want by taking $\alpha(R) - \alpha(0)$ small enough. Therefore, the range of possible values of K is 1/3 to infinity; the smaller values of K being obtained for small values of k, that is, for very stretchable radial fibers; and the large values of K being obtained for large k and small $\alpha(R) - \alpha(0)$, that is, for unstretchable and tense radial fibers.

Computation of the integrals. To compute the integrals, we shall suppose that $\cos \alpha(r)$ varies proportionally to the square of r:

$$\cos \alpha(r) = \cos \alpha(0) - [\cos \alpha(0) - \cos \alpha(R)] (r/R)^2. \qquad (38)$$

This relation holds when the first hypothesis of Helmholtz is satisfied [cf. equation (9)]. Using the notations of equation (31), we have

$$c(u) - c(v) = [\cos \alpha(0) - \cos \alpha(R)]R^{-2} [r^2(v) - r^2(u)],$$

$$c(u)r^2(v) - c(v)r^2(u) = \cos \alpha(0) [r^2(v) - r^2(u)], \qquad (39)$$

and the integrals (33) and (34) become

$$2R^2(NP - MQ) = \cos \alpha(0) [\cos \alpha(0) - \cos \alpha(R)]$$
$$\cdot R^{-2} \int \int [r^2(v) - r^2(u)]^2 \, du \, dv,$$

$$2(LN - M^2) = [\cos \alpha(0) - \cos \alpha(R)]^2$$
$$\cdot R^{-4} \int \int [r^2(v) - r^2(u)]^2 \, du \, dv.$$

Using also equation (35), we obtain

$$NP - MQ = \cos \alpha(0) [\cos \alpha(0) - \cos \alpha(R)] (LT - P^2),$$

$$LN - M^2 = [\cos \alpha(0) - \cos \alpha(R)]^2 (LT - P^2). \qquad (40)$$

Furthermore, to calculate the integrals L, N, P of equations (18) and $LT - P^2$ of equation (35), we shall neglect the curvature of the radial fibers; in other words, we shall assume that $\alpha(r)$ is constant:

$$L = \frac{\cos \alpha}{\sin^3 \alpha} R, \quad N = \frac{\cos^3 \alpha}{\sin^3 \alpha} R, \quad P = \frac{1}{3} \frac{\cos \alpha}{\sin^3 \alpha} R,$$

$$\qquad (41)$$

$$LT - P^2 = \frac{1}{2R^4} \frac{\cos^2 \alpha}{\sin^6 \alpha} \int_0^R \int_0^R (r^2 - s^2)^2 \, dr \, ds = \frac{4}{45} \frac{\cos^2 \alpha}{\sin^6 \alpha} R^2.$$

From equations (40), then, we obtain

$$NP - MQ = \frac{4 \cos^3 \alpha}{45 \sin^6 \alpha} \left[\cos \alpha (0) - \cos \alpha (R)\right] R^2,$$

$$\tag{42}$$

$$LN - M^2 = \frac{4 \cos^2 \alpha}{45 \sin^6 \alpha} \left[\cos \alpha (0) - \cos \alpha (R)\right]^2 R^2.$$

We still have to calculate the integral D of equation (36). Using relation (39), we obtain

$$R^4 D = \cos \alpha (0) \int \int \int \left[c(u) - c(v)\right] \left[r^2(w) - r^2(v)\right]$$
$$\cdot \left[r^2(u) - r^2(w)\right] du\, dv\, dw .$$

Therefore, by equation (37), we have

$$D = 0 . \tag{43}$$

Remark. The computation of the integrals (42) and (43) was based on the assumption that $\alpha(r)$ varies as the square of r. The values obtained, however, differ little from the values obtained with other hypotheses. For instance, if we had supposed that the radial fibers are arcs of a circle, which is to say that $\cos \alpha(r)$ varies as the first power of r, we would again have obtained the equations (42), except that the coefficient 4/45 would be replaced by 1/12. The value of D would not be zero, but

$$D = \frac{1}{2160} \frac{\cos^3 \alpha}{\sin^9 \alpha} \left[\cos \alpha (0) - \cos \alpha (R)\right]^2 R^3.$$

Computation of the coefficients K, A, B. We have approximately $R = X \tan \alpha$, and

$$\cos \alpha (0) - \cos \alpha (R) = \sin \alpha [\alpha (R) - \alpha (0)] .$$

Using these relations and equations (41), (42), and (43), we obtain by substitution in equations (26) and (28):

$$K = \frac{15 + 4 \cot \alpha [\alpha (R) - \alpha (0)]\, k}{45 + 4 [\alpha (R) - \alpha (0)]^2\, k} ,$$

$$A = \frac{45 \sin^2 \alpha + 45 \cos^2 \alpha\, k}{45 + 4 [\alpha (R) - \alpha (0)]^2\, k} \frac{\sin \alpha\, \phi}{\cos \alpha\, R} , \tag{44}$$

$$B = \frac{4}{15 + 4 \cot \alpha [\alpha (R) - \alpha (0)]\, k} \frac{\cos \alpha\, R}{\sin^3 \alpha\, \phi} .$$

Moreover, it may be convenient to express $\alpha (R) - \alpha (0)$ in these formulae in terms of the tensions in the drum, as we shall do now. We have from equations (7) and (13),

$$\frac{a(R) - a(0)}{\cos^2 \alpha} = \tan a(R) - \tan a(0) = \frac{2\pi}{\Gamma \cos \alpha} \int_0^s \gamma_c(s) \, ds.$$

Therefore,

$$a(R) - a(0) = 2\pi \cos \alpha \frac{\int_0^s \gamma_c(s) \, ds}{\Gamma}, \qquad (45)$$

where $\int_0^s \gamma_c(s) \, ds$ is the sum of the tensions of all the circular fibers and Γ is the sum of the tensions of all radial fibers.

If we suppose the radial fibers unstretchable ($k = \infty$) and that $\sin \alpha = 1$, and if we use equations (45) and $R = X \tan \alpha$, we can simplify the equations (44) into

$$K = \frac{\Gamma}{2\pi \int_0^s \gamma_c(s) \, ds}, \quad A = \frac{45}{4} \frac{\phi}{X} K^2, \quad B = 0. \qquad (46)$$

Conclusion. The dynamics of the ear drum lead to the equations (1), where the coefficients K, A, and B are given by equations (44) if we suppose the radial fibers stretchable, and by equations (46) if we suppose the radial fibers unstretchable. An interpretation of these equations has been given earlier.

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A MATHEMATICAL DESCRIPTION OF METABOLIZING SYSTEMS: II

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Some of the laboratory procedures available for determining the functions in the integral equation established in part I are discussed. The tracer or tagged molecule technique is shown to be especially promising including the use of "double tracer" molecules. Conversely, the integral equation may be a convenient device for correlating and integrating some of the work now being done with tracer molecules in biological systems.

In part I of this series of papers (Branson, 1946), the author established the integral equation

$$M(t) = M(0) \, F(t) + \int_0^t R(\theta) \, F(t-\theta) \, d\theta \qquad (1)$$

to describe the behavior of a metabolite, $M(t)$, in a system with rate, $R(t)$, and metabolizing function, $F(t)$. The usefulness of this equation will depend upon the experimental techniques available for determining any two of the functions in order that the third may be derived by solving the equation.

Although there are many laboratory techniques which will determine $M(t)$ as a function of t and control $R(t)$ so that $F(t)$ can be determined for certain specific conditions, the author is especially interested in determining these functions by the use of tagged or tracer atoms (radioactive or stable isotopes of ordinary chemical constituents of the metabolite). In all experiments, however, it is usually possible to plot $M(t)$ vs. t and determine by the usual mathematical techniques (Worthing and Geffner, 1943) a continuous function which will approximate the data within the experimental error.

The Determination of the Functions in the Integral Equation: In the typical experiment on metabolism, we are interested in the fate of some metabolite which we shall designate as $M(t)$. If our experiments are on mature, normal animals in nutritional equilibrium, we often find that the amount of the metabolite varies little if at all. The introduction of a tagged quantity of that metabolite, $M(t)$, reveals

that the constancy is only apparent. The equilibrium is dynamic, as has been so ably demonstrated by R. Schoenheimer and collaborators (Schoenheimer, 1946) with the stable heavy isotopes of hydrogen (H^2) and nitrogen (N^{15}). Hence when we assay for the metabolite, we are on the flat portion of a curve whose origin cannot be determined by examining $M(t)$ at the time of our experiment. According to equation (1), we have for this situation

$$M(0) [1 - F(t)] = \int_0^t R(\theta) F(t - \theta) d\theta, \qquad (2)$$

with R and F still to be determined. We need another independent relation for determining one of them.

The tracer atom technique gives us the required condition, for we need only inject a sample of tagged metabolite, $M^*(0)$, and follow its course in the same system or systems sufficiently similar. These data will give

$$M^*(t) = M^*(0) F(t). \qquad (3)$$

Since no additional tagged metabolite can enter, $R^* = 0$. Thus, by means of equations (2) and (3), we can determine the functions R and F.

The preceding formulation of equation (3) assumes that although the rate at which the tagged substance enters is different from that of the normal, the metabolizing functions are identical for both. If that were not true, then the system would be discriminating between the tagged and untagged molecules of otherwise identical chemical constitution. Within the experimental error of this work, the evidence is convincing that the biological system cannot distinguish the small differences in mass between the chemically similar units. There may exist slight differences in rates of diffusion and other physical phenomena.

If we are dealing with a metabolite or substance which is not in equilibrium, the procedure is the same except that then we must determine $M(t)$ and use equations (1) and (3) for R and F.

Treatment of some Data: As examples we shall consider some experiments using radioactively tagged molecules of J. G. Hamilton and M. H. Soley (1940), some experiments and theoretical developments by D. B. Zilversmit and collaborators (1943), and we shall allude to some experimental results of R. Schoenheimer and his collaborators (Schoenheimer, 1946).

J. G. Hamilton and M. H. Soley (1940) fed radioactive iodine (I^{131}) to a group of normal human subjects and observed by means of an external Geiger-Müller counter the emanations from the thyroid.

From the many types of empirical curves which may be fitted to their data, the writer selects

$$M(t) = C(1 - e^{-\alpha t}) \, e^{-\beta t}$$

with $C = 0.035 \, M^*(0)$, where $M^*(0)$ is the amount of tagged iodine fed. This choice of $M(t)$ describes the observed behavior satisfactorily and the expression is sufficiently tractable mathematically for straightforward integration in equation (1). From their data we see that the maximum of the curve is reached in about one day, hence $\alpha \sim 4.5$ days^{-1}. After 30 days, over 80 % of the radioactive iodine remained in the thyroid, hence $\beta \sim 0.006$ day^{-1}. Inasmuch as there was no radioactive iodine originally present, equation (1) now becomes:

$$C(1 - e^{-\alpha t}) \, e^{-\beta t} = \int_0^t R(\theta) \, F(t - \theta) \, d\theta \, .$$

Although we cannot write an equation such as equation (3) on the basis of the data, the fact that the radioactive iodine slowly leaves the thyroid limits the possibilities for $F(t)$. Upon integration and by use of this qualitative information on $F(t)$, we have

$$F(t) = e^{-\beta t},$$
$$R(t) = \alpha \, C \, e^{-(\alpha + \beta) t}. \tag{4}$$

Thus we may conclude on the basis of our formulation that the metabolizing function describing the history of iodine in the thyroid is a slowly decreasing function of time, while the rate function decreases rapidly with time. Although the parameters α and β are empirical and are not related to physiological processes, nevertheless, their values may be important clues in detecting malfunctioning of the thyroid.

The example given by D. B. Zilversmit and his collaborators (Zilversmit, Enteman and Fishler, 1943; Zilversmit, Enteman, Fishler and Chaikoff, 1943) is an example of the general problem of the conversion of A into B where A is called the precursor of B. A may be produced by complex reactions and B may be lost through others. We shall assume only that for each unit of A which disappears a unit of B appears. If A and B are tagged substances, we shall have none of either present initially, hence

$$A^*(t) = \int_0^t R(\theta) \, F(t - \theta) \, d\theta \, ,$$

$$B^*(t) = \int_0^t R_1(\theta) \, F_1(t - \theta) \, d\theta \, .$$

If we assume that the transformation of A into B is an irreversible, first order reaction, chemical kinetics states that $R_1(\theta) = CA^*(\theta)$, whence

$$B^*(t) = C \int_0^t \cdot \left[\int_0^\theta R(\phi) \, F(\theta - \phi) \, d\phi \right] F_1(t - \theta) \, d\theta .$$

The resulting expression for $B^*(t)$ is complicated as one would expect in the absence of additional simplifying assumptions. There are three functions to be determined, R, F and F_1. We shall need one additional relation in order to determine the functions uniquely. One approach would be to follow the behavior of A^* and B^* in a similar system where it is injected. For such a system $A^*(t) = A^*(0)F(t)$.

The systems treated by D. B. Zilversmit and collaborators (Zilversmit, Enteman and Fishler, 1943; Zilversmit, Enteman, Fishler and Chaikoff, 1943) are simpler. Their general system $(A \to B)$ is described in our integral equation formulation by the equations

$$A^*(t) = \int_0^t R(\theta) \, F(t - \theta) \, d\theta ,$$

$$B(0) = B(0) \, F_1(t) + \int_0^t R_1(\theta) \, F_1(t - \theta) \, d\theta ,$$

$$B^*(t) = C \int_0^t A^*(\theta) \, F_1(t - \theta) \, d\theta ,$$

which state that the amount of B present is constant, and $R = CA$ which is constant if the amount of A is constant. Thus from following the courses of A^*, B^*, and determining B in one system and either A in the same system, or A^* or B^* in a similar system, we shall have enough relations to determine the R's and F's. If we are interested only in the R and F associated with B, we need know only $A^*(t)$, $B^*(t)$, and $B(0)$.

Their experiments on the turnover rate of phospholipids in the plasma of the dog with radioactive phosphorus follow the conditions for the system described by equation (9) of part I for the ordinary phosphorus and $B^*(t) = B^*(0) \, F(t)$ for the radioactive. Since R is constant, $F(t) = \exp(-R/M)t$.

The curves describing the atom percent deuterium uptake of cholestorol in mice (Schoenheimer, 1946), as well as other experimental results with stable isotopes (Schoenheimer, 1946), are expressed with acceptable accuracy by $M(t) = C(1 - e^{-at}) \, e^{-\beta t}$, with $\alpha >> \beta$, which gives expressions similar to equations (4) for the metabolizing function and the rate.

The application of double tracer techniques, e.g. using radioactive

carbon (C^{14}) and "heavy" carbon (C^{13}), H^3 and H^2, etc., to label the molecules would be particularly advantageous in determining the functions in equation (1). We could determine simultaneously $A^*(t)$ in

$$A^*(t) = \int_0^\tau R(\theta) \, F(t-\theta) \, d\theta$$

and $\bar{A}^*(t)$, where the bar indicates the second type of tagged molecule, in $\bar{A}^*(t) = \bar{A}^*(0) \, F(t)$. Thus by using two differently tagged, but chemically similar, molecules in a single system, we would have the two equations necessary to determine both R and F.

As a specific example of the double tracer technique let us consider an experiment on the metabolism of methionine in the rat or mouse. We can feed homocystine labelled with radioactive sulfur (S^{35}) and methionine labelled with a stable rare isotope of sulfur (S^{33} or S^{34}). It may be necessary to feed some choline or betaine in order that the animals may synthesize the methionine from the homocystine. From a series of animals, we may isolate methionine from the body tissue. Radioactive assays will give $A^*(t)$, the radioactive methionine synthesized from the homocystine. Determinations with the mass spectrometer will give $\bar{A}^*(t)$, the amount of methionine remaining from the labelled amount fed. There are severe experimental difficulties in the determination of sulfur; nevertheless, the procedure seems practicable and such experiments are being planned in our laboratory.

The preceding discussion reveals how the tracer element technique may be used in determining the needed functions in equation (1). It may be, however, that the chief significance of equation (1) will be its value in integrating and correlating some of the work now being done with biological systems using the tracer element and other techniques.

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A MATRIX CALCULUS FOR NEURAL NETS: II

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In a previous paper a method was given by which the efferent activity of an idealized neural net could be calculated from a given afferent pattern. Those results are extended in the present paper. Conditions are given under which nets may be considered equivalent. Rules are given for the reduction or extension of a net to an equivalent net. A procedure is given for constructing a net which has the property of converting each of a given set of afferent activity patterns into its corresponding prescribed efferent activity pattern.

In a previous publication (Landahl and Runge, 1946), we defined a structure matrix $F = |f_{jk}|$ related to a neural net of N neurons. Each element f_{jk} of F is a measure of the potential action of a neuron N_j on a neuron N_k. The matrix F contains four non-zero sections F_X, F_R, F_I and F_E which determine respectively the relationships afferent-efferent, afferent-internal, internal-internal and internal-efferent. We also defined a normalizing operator G and the activity vector $a(t) = r(t) + i(t) + e(t)$ which specifies the activity of all neurons of the net at time t. The $(1 \times \rho)$ vector $r(t)$ describes the activity of the ρ receptor neurons at time t, the $(1 \times \iota)$ vector $i(t)$ describes the activity of the internal neurons, while the $(1 \times \varepsilon)$ vector $e(t)$ describes the activity of the efferent neurons at time t. An equation was given by which any $a(t)$ could be determined from a knowledge of the sequence of r's and a set of initial conditions [*loc. cit.* equation (10)].

We introduce some definitions. Suppose that two nets, with N' and $N''(> N')$ neurons, each containing the same set of afferents and efferents, have the property that if $r_\sigma(t) = 0$ for all $t < 0$, then for any sequence $\mathcal{R}_\sigma(r) = [r_\sigma(0), r_\sigma(1), \cdots]$ there results a sequence $\mathcal{E}_\sigma(e)$ of e_σ's, the same for both nets. Then N' is a reduced equivalent net of N'', and N'' is an expanded equivalent net of N'. If the above holds, not for every sequence, but only for a given set of sequences of r's, then we may refer to N'' as an expanded adequate net of N' over the set of pairs of sequences $\mathcal{R}_\sigma$, $\mathcal{E}_\sigma$.

Consider two matrices F and F'' of orders $(\rho + \iota + \varepsilon)$ and $(\rho + \iota' + \varepsilon)$ which have no internal neurons in common. The matrix

given by their direct sum represents the sum of the two nets if there are no neurons in common. On rearranging rows and columns, this matrix can be transformed into a square matrix of order $\rho + \rho' + \iota + \iota' + \varepsilon + \varepsilon'$. If the two nets have the same set of afferents and efferents, this matrix can be reduced to a square matrix of order $\rho + \iota + \iota' + \varepsilon$ by adding the two rows which represent the same neuron and adding the corresponding columns, then deleting the duplicate row and column. The resulting matrix shall be referred to as the extended sum of F and F'. It may be written as:

$$
\begin{matrix}
0 & F_R & F_X \\
0 & F_I & F_E \\
0 & 0 & 0
\end{matrix}
\;(+)\;
\begin{matrix}
0 & F'_R & F'_X \\
0 & F'_I & F'_E \\
0 & 0 & 0
\end{matrix}
=
\begin{matrix}
0 & F_R & F'_R & F''_X \\
0 & F_I & 0 & F_E \\
0 & 0 & F'_I & F_E \\
0 & 0 & 0 & 0
\end{matrix}
\qquad (1)
$$

where $F''_X = F_X + F'_X$.

   If F and F' represent equivalent nets, then their extended sum represents an extended adequate net of either primary net. But if $F_X = F'_X = 0$, then the extended sum represents an equivalent net if for each efferent column of the final matrix it is true that not both columns of the submatrices F_E and F'_E contain elements such that the sum of any group in the column lies between zero and one. If matrices F and F' contain neither finite negative elements nor proper fractions in the sections F_X and F_E, or if the sections contain only integers, then their extended sum represents an extended equivalent net. If F and F' represent equivalent nets, if the simplifying rules have been applied to eliminate non-functional elements, and if f_{re} denotes an element of F_X, then f_{re} and f'_{re} are both greater than or equal to one, both equal to zero, both arbitrarily large negative elements, both proper fractions, or are both finite negative elements. If F_X and F'_X contain no proper fractions or finite negative elements, then $F_X = F'_X$ and F''_X may be replaced by F_X in equation (1).

   We may now write the following efferent separation theorem **(I)**: *Any net represented by the square matrix* F' *of order* $\rho + \iota' + \varepsilon$ *can be replaced by an expanded equivalent net,* the duplicated net, *represented by a square matrix* F" *of order* $\rho + \varepsilon\iota' + \varepsilon$ *which is the extended sum of* F'$_X$, F'$_1$, $\cdots$ F'$_e$, $\cdots$ F'ε *where* F'$_e$ *is* F' $-$ F'$_X$ *with all of the efferent columns except* e *replaced by columns of zeros.*

   From an inspection of F'' it becomes clear that $a'(t)$ and $a''(t)$ differ only in that the internal vector $\iota''(t)$ is a vector $(1 \times \iota\varepsilon)$ which results from extending the $(1 \times \iota)$ vector $\iota'(t)$ by repeating it ε times.

   The following rules may be useful in simplifying computations and enabling reductions to be made according to rules given subsequently:

1. If any column in the structure matrix F contains only one non-zero element, this element may be replaced by one if it is greater than one, zero if less than one.

2. If any column in F contains no negative elements except arbitrarily large ones, then any element greater than one can be replaced by one.

3. Any non-functional element f_{jk} may be deleted from F. Such an element is less than one, and satisfies the condition $(S_k + f_{jk})G = S_k G$ where S_k is the sum of any group of elements except f_k in column k of F.

We next give some rules which result in reduced equivalent nets:

1. If any row of the structure matrix F representing an internal neuron contains only zero elements, that row, the corresponding column in F and the corresponding space in the activity vector a may be deleted.

2. If any column of F representing an internal neuron contains only zero elements, or if the sum of the positive elements of that column is less than one, that column, its corresponding row in F and the corresponding space in a, may be deleted.

3. If any two columns in F representing internal neurons are identical, one of these columns and its corresponding row in F and the corresponding space in a may be deleted, provided that the row corresponding to the column not omitted is replaced by the matrix sum of these two rows.

4. Suppose that in the matrix F, two rows α and β are identical and that each represents an internal neuron. Consider the following set of conditions:

a) The rows of α and β contain no proper fractions or finite negatives.

b) Neither of the corresponding columns α and β contains finite negative elements.

c) Each column γ, for which the elements of rows α and β are both greater than or equal to one, contains no finite negative numbers.

d) The fractional elements are identically placed in each column, and if there are arbitrarily large negatives, these occur in pairs, except that one column may contain additional negatives if it contains no elements greater than or equal to one.

e) Neither column α nor column β contains arbitrarily large negative elements unless they occur in the same rows for both columns.

f) Either column α or column β contains no elements which are proper fractions.

Then, if conditions (a), (b) and (c) hold, together with either condition (d) or conditions (e) and (f), one can delete one row and its corresponding column in F and the corresponding space in a if the two columns are combined in such a way that the algebraically larger of corresponding elements is retained in each case.

It is very likely to be the case that the duplicated net of theorem (I) can be reduced to a smaller net which is still an expanded equivalent net of the original net. Suppose that the structure matrix of the original net contained no pair of rows or pair of columns which are equal. Then in the duplicated net, no two columns are equal, but there may well be rows which are equal. Suppose this is the case and a reduction is made. Then the corresponding F'_I in the diagonal of F''_I, the corresponding section F'_R and the corresponding section F'_E of F'' are altered. Suppose successive reductions are made only if pairs of identical rows pass through the same F'_I in the diagonal of F''_I. When there are no more obvious reductions of this kind left to be made, each of the non-zero sections of F'', except F''_X, may have been altered. Thus we may write the following theorem (II):

For any net of N' *neurons,* $N' = \rho + \iota + \varepsilon$, *with a corresponding structure matrix* F', *there is an extended equivalent net, a separated net, of* N^* *neurons,* $N^* = \rho + \iota_1 + \cdots + \iota_a + \cdots \quad \iota_\varepsilon + \varepsilon$, *which has a structure matrix* F^* *equal to* F'_X *plus the extended sum of* ε *matrices represented by the* $(\rho + \iota_a + \varepsilon)^2$ *matrix* F_a *which has zeros in all the last* ε *columns except column* $\rho + \iota_a + a$, *the first* ρ *elements of this column being zeros also.*

The resulting matrix F^* is one in which F^*_I is given by diag $\{F_{1I}, \cdots, F_{aI}, \cdots, F_{\varepsilon I}\}$, $F^*_X = F'_X$, and F^*_E may be written as diag $\{b_1, \cdots, b_a, \cdots, b_\varepsilon\}$, where b_a is a $(\iota_a \times 1)$ column vector.

The above theorem reduces the problem of the construction of a net with ε efferents to the problem of the construction of a net with one efferent. Having constructed a net for each efferent alone, the total net can then be determined by theorem (II). We shall find, however, a method of constructing nets which will not require use of the above theorem. We pass now to this problem:

Suppose that a certain sequence $\mathcal{R}_\sigma(r)$ of r's leads to a finite sequence $\mathcal{E}_\sigma(e)$ of e's, and that a number of such pairs of sequences is known empirically. It will be assumed that the net is always at rest when any afferent sequence is initiated. We wish to construct a net for which the structure matrix $F(\mathcal{R}, \mathcal{E})$ is such that each $\mathcal{R}_\sigma$ of a set $\mathcal{R}$ of sequences of r's leads to the appropriate sequence $\mathcal{E}_\sigma$ of e's. Suppose that $e_\sigma(1)$ is the first non-zero e. If a particular sequence $\mathcal{R}_\sigma(r)$ leads to a particular $\mathcal{E}_\sigma(e)$, we can write this sequence of r's, $r_\sigma(-l'), \cdots, r_\sigma(-\tau), \cdots, r_\sigma(0), \cdots, r_\sigma(l'')$ which results in a

sequence $e_\sigma(1)$, $e_\sigma(2)$, $\cdots$, $e_\sigma(t)$, $\cdots$, $e_\sigma(l''')$, as a set of sequences in which $r_\sigma(-l')$, $\cdots$, $r_\sigma(0)$ results in $e_\sigma(1)$, and $r_\sigma(-l')$, $\cdots$, $r_\sigma(1)$ results in $e_\sigma(2)$, and so forth. Now let $\mathcal{R}_1$ be the first sequence, $\mathcal{R}_\sigma$ be sequence σ, and $\mathcal{R}_s$ be the last sequence, all sequences having been ordered. Let the time be adjusted for each sequence so that the last member of $\mathcal{R}$ is $r(0)$, and each sequence $\mathcal{E}(e)$ contains but one element $e(1)$. Let $l+1$ be the longest series of r's so that, in general, sequence $\mathcal{R}_\sigma$ will begin with $r_\sigma(-l)$ and end with $r_\sigma(0)$, and have the general term $r_\sigma(-\tau)$.

Now $r_\sigma(-\tau)$ will always be composed of zeros and ones, but some of these may not be known. Thus there will be some number $m_{\sigma\tau}$, ones, some number of zeros and a number of unknowns x. Similarly $e_\sigma(1)$ will contain elements which may be one, zero or x.

For the following construction, the occurrence of a one in the r-th element of $r_\sigma(-\tau)$ implies that the r-th efferent must act at time $t = -\tau$ in order that $e_\sigma(1)$ have its given value. The occurrence of a zero means that the corresponding afferent must not act at time $t = -\tau$ if $e_\sigma(1)$ is to have the value given. The occurrence of an x implies that it is immaterial whether or not the corresponding element acted at $t = -\tau$. It is understood that all $r(t)$ vectors for $t < -l$ contain only x's. In the case of the efferent vector, e, the occurrence of a unity in the e-th element implies that the sequence $\mathcal{R}_\sigma$ does cause the e-th efferent to act at $t = 1$, whereas a zero in this element implies that sequence $\mathcal{R}_\sigma$ prevents its action even though some part of $\mathcal{R}_\sigma$ could otherwise produce activity. But an x in $e_\sigma(1)$ means that it is immaterial whether or not this element occurs as a result of $\mathcal{R}_\sigma$, though generally it may be considered that $\mathcal{R}_\sigma$ simply fails to produce activity in the corresponding efferent at $t = 1$.

Define an operator $\mathcal{B}_R$ which acts on a $(1 \times \rho)$ afferent activity vector $r_\sigma(-\tau)$ such that $\mathcal{B}_R\{r_\sigma(-\tau)\}$ is a $(\rho \times \varepsilon)$ matrix made up of equal column vectors whose elements are obtained from $r_\sigma(-\tau)$ in the following manner. Let n_σ be the number of vectors in $\mathcal{R}_\sigma$ which contain at least one unity. An element one in $r_\sigma(-\tau)$ is changed to $1/m_{\sigma\tau}n_\sigma$, an element x is changed to zero, and an element zero is changed to $-\delta$ where δ is an arbitrary positive quantity. If $r_\sigma(-\tau)$ contains at least one unity, then $r_\sigma(-\tau)$ $\mathcal{B}_R\{r_\sigma(-\tau')\}$ is a row vector of repeated elements $1/n_\sigma$ if $r_\sigma(-\tau) = r_\sigma(-\tau')$, otherwise each element is less than $1/n_\sigma$. When $r_\sigma(-\tau)$ contains no ones, then the elements of $r_\sigma(-\tau) \mathcal{B}_R\{r_\sigma(-\tau')\}$ are all zero if $r_\sigma(-\tau) = r_\sigma(-\tau')$, otherwise each element is less than or equal to zero. In a somewhat similar manner, define $\mathcal{B}_E$ as an operator which acts on a $(1 \times \varepsilon)$ efferent activity vector e such that $\mathcal{B}_E\{e\}$ is a $(\varepsilon \times \varepsilon)$ diagonal matrix whose diagonal elements are obtained from e by changing zero to $-\delta$, x to

zero, ones remaining unchanged.

We shall next define an operator which extends a structure matrix by adding an element between each afferent and the neurons being acted upon by afferents, displacing these connections. If F is any structure matrix, then the afferent extending operator T_R is defined by the relation:

$$\text{If } F = \begin{matrix} 0 & F_R & F_X \\ 0 & F_I & F_E \\ 0 & 0 & 0 \end{matrix}, \text{ then } T_R F = \begin{matrix} 0 & 1^\rho & 0 & 0 \\ 0 & 0 & F_R & F_X \\ 0 & 0 & F_I & F_E \\ 0 & 0 & 0 & 0 \end{matrix}, \quad (2)$$

where 1^ρ is a unit matrix of order ρ. The operator T_R is distributive with respect to extended sums if matrices which represent equivalent nets are said to be equal.

Let F' be a structure matrix such that the sequence $\mathcal{R}_\sigma$ less the last vector $r_\sigma(0)$, which we assume to contain no ones, results in $e_\sigma(0) = (1, 1, 1 \cdots, 1)$; that is, $e_\sigma(1)$ occurs one unit of time sooner than it should, and such that every efferent acts. Then it can be seen that

$$F'_\sigma = X\{r_\sigma(-1)\} + T_R X\{r_\sigma(-2)\} (+) \cdots (+) T_R{}^{l-1} X\{r_\sigma(-l)\} \quad (3)$$

$$= \sum_{\tau=1}^{s}{}^{(E)} T_R{}^{\tau-1} X\{r_\sigma(-\tau)\},$$

where $X\{r_\sigma(-\tau)\}$ is a structure matrix, $(\rho + \varepsilon) \times (\rho + \varepsilon)$, which contains $\mathcal{B}_R\{r_\sigma(-\tau)\}$ in its upper right hand corner but is elsewhere zero. The summation sign with a superscript (E) will be used to denote an extended sum.

Now F_σ will contain a submatrix $F_{\sigma E}$ in which each column contains $\mathcal{B}_R\{r_\sigma(-1)\}$, $\mathcal{B}_R\{r_\sigma(-2)\}$, $\cdots$, and $\mathcal{B}_R\{r_\sigma(-l)\}$. Thus each efferent will act as a result of a sequence $\mathcal{R}'_\sigma$ if, and only if, the sum $r'_\sigma(-1) \mathcal{B}_R\{r_\sigma(-1)\} + \cdots + r'_\sigma(-l) \mathcal{B}_R\{r_\sigma(-l)\}$ is greater than or equal to unity in any element. Now this sum cannot exceed $n_\sigma(1/n_\sigma)$ and will equal unity if, and only if, $r'_\sigma(-\tau) = r_\sigma(-\tau)$ for every τ; hence, only the sequence $\mathcal{R}_\sigma$ is effective.

Analogous to the operator T_R, we can define an operator T_E, which extends the structure on the efferent side, by

$$T_E F = \begin{matrix} 0 & F_R & F_X & 0 \\ 0 & F_I & F_E & 0 \\ 0 & 0 & 0 & 1^\varepsilon \\ 0 & 0 & 0 & 0 \end{matrix}, \quad (4)$$

the quantity 1^ε being the unit matrix of rank ε.

From the fourth rule for reducing a matrix it follows that $T_E(F' \; (+) \; F'') = T_E F' \; (+) \; T_E F''$ if F'_x, F''_x, F'_E, F''_E contain no proper fractions or negative elements. Evidently, then, if $F' = T_E F$ and $F'' = T_E \overline{F}$, T_E will be distributive with respect to F' and F''.

It will be necessary to use a more special operator T_e which acts on a structure matrix as above but in which $\mathbf{1}^\varepsilon$ is replaced by the diagonal matrix $\mathcal{B}_E\{e\}$. Then $T_e F'_\sigma$ is a structure matrix such that the sequence $\mathcal{R}_\sigma$, and only this sequence [$r_\sigma(0)$ containing no ones], results in $e(1)$, with the exception that $r_\sigma(0)$ has no effect. Let $X\{r_\sigma(0), e_\sigma(1)\}$ be a matrix of suitable order, which is zero everywhere except in the last ε columns of the first ε rows, this non-zero submatrix being $[\mathcal{B}_R\{r_\sigma(0)\}][\mathcal{B}_E\{e_\sigma(1)\}]$. This matrix takes into account the effect of the vector $r_\sigma(0)$. Thus adding this to $T_e F'_\sigma$ results in a matrix F_σ representing a net in which the afferent sequence $\mathcal{R}_\sigma$ results in the efferent activity vector $e_\sigma(1)$. The extended sum of these matrices represented by F_σ is then the structure matrix desired, and we have the following result:

If each of a set $\mathcal{R}$ of sequences $\mathcal{R}_\sigma$ of afferent activity vectors results in a corresponding sequence $\mathcal{E}_\sigma$ of afferent activity vectors of a set $\mathcal{E}$, and these have been written in such a way that each afferent sequence contains only one vector, and if the last vector of each sequence of $\mathcal{R}$ contains no ones or if we choose to ignore them, and if $e_\sigma(1)$ contains no zeros whenever $r_\sigma(0)$ contains zeros, then the structure which converts a sequence of $\mathcal{R}$ into a sequence $\mathcal{E}$ is represented by the matrix $F(\mathcal{R}, \mathcal{E})$ given by

$$F(\mathcal{R}, \mathcal{E}) = \sum_{\sigma=1}^{s} X\{r_\sigma(0), e_\sigma(1)\} + \sum_{\sigma=1}^{s}{}^{(E)} T_e$$

$$\cdot \left[\sum_{\tau=1}^{l}{}^{(E)} T_R{}^{\tau-1} X\{r_\sigma(-\tau)\} \right], \tag{5}$$

the operators and symbols having been defined above. If no e contains a zero, then we may also write

$$F(\mathcal{R}, \mathcal{E}) = \sum_{\sigma=1}^{s} X\{r_\sigma(0), e_\sigma(1)\} + \sum_{\sigma=1}^{s}{}^{(E)} T_E$$

$$\cdot \left[\sum_{\tau=1}^{l}{}^{(E)} T_R{}^{\tau-1} X\{r_\sigma(-\tau), e_\sigma(1)\} \right]. \tag{6}$$

If the last activity vectors contain ones, then the above method can be modified to give a result under certain conditions. If it is the case that in forming the sum of $X\{r_\sigma(0), e_\sigma(1)\}$ over σ, no element

is the result of adding a positive term with either a negative or a positive term, unless both are greater than or equal to one, and if no $e_\sigma(1)$ contains zeros, then $F(\mathcal{R}, \mathcal{E})$ can be written as in equation (6) but with $\mathcal{T}_E$ replaced by $\mathcal{T}_R$. Since $\mathcal{T}_R(F_1 (+) F_2) = \mathcal{T}_R F_1 (+) \mathcal{T}_R F_2$ after reducing by rule (2), the operator $\mathcal{T}_R$ outside the brackets can be brought under the second summation sign. Since an ordinary sum in the first term of equation (6) cannot be confused with the extended sum, we may then write for this case

$$F(\mathcal{R}, \mathcal{E}) = \sum_{\sigma=1}^{s}{}^{(E)} \sum_{\tau=0}^{l} \mathcal{T}^\tau{}_R \, X\{r_\sigma(-\tau), e_\sigma(1)\}. \tag{7}$$

More generally, however, when $r_\sigma(0)$ contains ones in a certain subgroup of sequences, $\sigma = s' + 1, \cdots, s$, then instead of equation (7) we may write an equation in which the sum over σ from 1 to s' is given as in equation (5), while the sum over σ from $s' + 1$ to s is given as in equation (7). This gives a more general equation for the construction of a net:

$$F(\mathcal{R}, \mathcal{E}) = \sum_{\sigma=1}^{s'} X\{r_\sigma(0), e_\sigma(1)\}$$

$$(+) \sum_{\sigma=1}^{s'}{}^{(E)} \mathcal{T}_e \left[\sum_{\tau=1}^{l}{}^{(E)} \mathcal{T}_R{}^{\tau-1} X\{r_\sigma(-\tau)\} \right] \tag{8}$$

$$(+) \sum_{\sigma=s'+1}^{s}{}^{(E)} \sum_{\tau=0}^{l} \mathcal{T}_R{}^\tau X\{r_\sigma(-\tau), e_\sigma(1)\}.$$

If no $e(1)$ contains a zero, $\mathcal{T}_e$ may be replaced by $\mathcal{T}_E$ in equation (8):

Let the superposition of two sequences be a sequence formed by combining corresponding elements $(1, x$ or $0)$ of corresponding vectors as follows: The combination of an element with itself is the element itself. The combination of an x with any element is that element with which x is combined. If the sequence is an efferent, then the combination of a zero and a one is the element zero. If the sequence is an afferent, then if zero and one combine in any element, the superposition is a null sequence. The superposition of sequences is commutative and associative.

Let a set of afferent and efferent sequences $(\mathcal{R}, \mathcal{E})$ be given. Let $(\mathcal{R}, \mathcal{E})_T$ be the set containing $(\mathcal{R}, \mathcal{E})$ and all its non-null superpositions. Then we may refer to a net as being structurally equivalent to a set of sequence pairs $(\mathcal{R}, \mathcal{E})$ if every $\mathcal{R}_\sigma$ in $(\mathcal{R}, \mathcal{E})_T$ applied to the net results in $\mathcal{E}_\sigma$ but every other afferent sequence results in $\mathcal{E} = 0$. If the above holds for every pair in $(\mathcal{R}, \mathcal{E})$ but not for all superpositions, then we may refer to the net as being structurally equivalent to $(\mathcal{R}, \mathcal{E})$ in a stronger sense. Similarly, we may refer to a net as being

adequate with respect to $(\mathcal{R}, \mathcal{E})$ if each given afferent sequence applied to the net results in its corresponding efferent sequence but some other sequences, not in $\mathcal{R}$, result in non-null efferent sequences.

If equation (8) reduces to equation (5) or (6), then the net constructed is structurally equivalent to $(\mathcal{R}, \mathcal{E})$. The net obtained from equation (8) may be structurally equivalent even though that constructed by equation (7) is only adequate; but the net obtained from equation (7) may be equivalent in a stronger sense. The net obtained from equation (8) will be equivalent, perhaps in the stronger sense, if the sum of the elements of every efferent column of the structure matrix which contains proper fractions is unity.

Under the following conditions it will not be possible by the above method to construct a net which is even structurally adequate. Let σ, σ', r, and e be subscripts which can take on any value in their respective ranges $[(1, \cdots, s), (1, \cdots, s), (1, \cdots, \rho), (1, \cdots, \varepsilon)]$. The conditions are then: a) $r_\sigma(0)$ and $e_\sigma(1)$ both contain zero elements, and b) the scalar elements $r_{\sigma r}(0) = e_{\sigma e}(1) = 1$, while either $r_{\sigma' r}(0) = 1$ and $e_{\sigma' e}(1) = 0$ or $r_{\sigma' r}(0) = 0$ and $e_{\sigma' e}(1) = 1$.

In constructing a net, one may use the rules for reducing nets but not the rules for changing elements. Since the quantity $-\delta$ is of arbitrary magnitude, one may choose it to be arbitrarily large. In matrices, this will be indicated simply by a minus sign. By choosing δ's large, the probability of being able to reduce the net is increased. It should also be noted that the use of the operator $\mathcal{T}_e$ in equation (5) results in ε identical columns of which all but one can be eliminated if the corresponding columns are added. This results in a row vector in place of the diagonal matrix, the elements of the row being the same as the elements of the original diagonal submatrix.

The construction of a net from equation (8) may be illustrated by an example from W. S. McCulloch and W. Pitts (1943) cited previously (Landahl and Runge, 1946). In this case we have $\mathcal{R}_1 = [(x, 1), (x, 0), (xx)]$, $e_1 = (1, x)$; $\mathcal{R}_2 = (1, x)$, $e_2 = (1, x)$ and $\mathcal{R}_3 = [(x, 1), (x, 1)]$, $e_3 = (x, 1)$. Readjusting the time so that each e is $e(1)$, then $\mathcal{B}_R\{r_1(0)\} = 0$, $\mathcal{B}_R\{r_1(-1)\} = \begin{vmatrix} 0 & 0 \\ - & - \end{vmatrix}$, $\mathcal{B}_R\{r_1(-2)\} = \begin{vmatrix} 0 & 0 \\ 1 & 1 \end{vmatrix}$, $\mathcal{B}_R\{r_2(0)\} = \begin{vmatrix} 1 & 1 \\ 0 & 0 \end{vmatrix}$, $\mathcal{B}_R\{r_3(0)\} = \begin{vmatrix} 0 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{vmatrix}$, $\mathcal{B}_R\{r_3(-1)\} = \begin{vmatrix} 0 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{vmatrix}$. Similarly $\mathcal{B}_E\{e_1\} = \mathcal{B}_E\{e_2\} = \begin{vmatrix} 1 & 0 \\ 0 & 0 \end{vmatrix}$ and $\mathcal{B}_E\{e_3\} = \begin{vmatrix} 0 & 0 \\ 0 & 1 \end{vmatrix}$. The F_x section of the sum $X\{r_\sigma(0), e_\sigma(1)\} = 0 + \begin{vmatrix} 1 & 0 \\ 0 & 0 \end{vmatrix} + \begin{vmatrix} 0 & 0 \\ 0 & \frac{1}{2} \end{vmatrix} = \begin{vmatrix} 1 & 0 \\ 0 & \frac{1}{2} \end{vmatrix}$.

Now $\mathcal{T}_R\, X\, \{r_1(-2)\}$ is a (5×5) matrix whose F_R, F_E and F_I sections are, respectively, $\begin{vmatrix} 0 \\ 1 \end{vmatrix}$, $|1\ 1|$ and zero. Thus the term due to sequence $\mathcal{R}_1$, $\mathcal{T}_e\,[X\{r_1(-1)\}\,(+)\,\mathcal{T}_R\, X\{r_1(-2)\}]$, is a (7×7) matrix which reduces to the (6×6) matrix for which the sections F_R, F_E and F_I are, respectively, $\begin{vmatrix} 0 & 0 \\ 1 & - \end{vmatrix}$, $\begin{vmatrix} 0 & 0 \\ 1 & 0 \end{vmatrix}$, $\begin{vmatrix} 0 & 1 \\ 0 & 0 \end{vmatrix}$. The last term $\mathcal{T}_R\, X\, \{r_3(-1),\, e_3(1)\}$ is a (5×5) matrix whose F_R, F_E and F_I sections are $\begin{vmatrix} 0 \\ 1 \end{vmatrix}$, $|\,0\ \tfrac{1}{2}\,|$, and zero. The extended sum of the above matrices leads to a (7×7) matrix in which there are two identical columns. Elimination of one row and column leads to a matrix which is identical to that previously written (Landahl and Runge, 1946) to represent the net of W. S. McCulloch and W. Pitts (1943), except for the negative element. In this case this element is arbitrary, while by the other construction it is an arbitrarily large negative, though it was written as minus one for convenience. It is evident by inspection that the magnitude of this element does not affect the equivalence of the nets in this case. The resulting net is structurally equivalent to the given set of pairs of sequences.

If, instead of using equation (8) for constructing the net, equation (7) had been used, then the resulting matrix would differ from that obtained above in that the element of row 2 and column 4 would be zero instead of negative, while the element of row 3 column 5 would be negative instead of zero. This net is structurally equivalent in the stronger sense to the given set of pairs of sequences.

LITERATURE

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